

PROTOZOOLOGY

KUDO

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PROTOZOOLOGY

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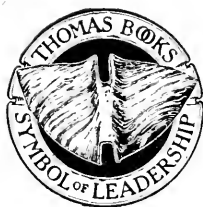
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Enlarged and completely rewritten edition of
HANDBOOK OF PROTOZOOLOGY

With two hundred and ninety-one illustrations



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“*The revelations of the Microscope are perhaps not
excelled in importance by those of the telescope.
While exciting our curiosity, our wonder
and admiration, they have proved of
infinite service in advancing our
knowledge of things
around us.*”

LEIDY

Preface

THE present work is similar in its primary aim to that of its predecessor, *Handbook of Protozoology* (1931), in presenting "introductory information on the common and representative genera of all groups of both free-living and parasitic Protozoa," to advanced undergraduate and graduate students in zoology in colleges and universities. With the expansion of courses in protozoology at the University of Illinois and elsewhere, it seemed advisable to incorporate more material for lecture and discussion, in addition to the enlargement of the taxonomic section. The change of the text-contents has, therefore, been so extensive that a new title, *Protozoology*, is now given.

Chapters 1 to 6 deal with introduction, ecology, morphology, physiology, reproduction, and variation and heredity, of Protozoa. Each subject-matter has been considered in the light of more recent investigations as fully as the space permitted. Selection of material from so great a number of references has been a very difficult task. If any important papers have been omitted, it was entirely through over-sight on the part of the author.

The taxonomic portion (Chapters 7 to 43) has also been completely rewritten and enlarged. Numerous genera and species, both old and new, have been added; synonymy of genera and species has as far as possible been brought down to date; new taxonomic arrangement of major and minor subdivisions in each class has resulted in numerous changes. The class Ciliata has completely been reclassified, following Kahl's admirable work on free-living ciliates (1930-1935); however, unlike the latter, all parasitic ciliates have also been considered in the present work.

The author continues to believe that good illustrations are indispensable in this kind of work, since they are far more easily comprehended than lengthy descriptions. Therefore, many old illustrations have been replaced by more suitable ones and numerous new illustrations have further been added. All illustrations were especially prepared for this work and in the case of those which have been redrawn from illustrations found in published papers, the indebtedness of the author is indicated by mentioning the names of the investigators from whose works the illustra-

tions were taken. In order to increase the reference value, all figures are accompanied by scales of magnification which are uniformly somewhat greater than those of *Handbook of Protozoology*, since the microscope now used in the class-room has been improved upon in recent years.

The list of references appended to the end of each chapter has been enlarged and is meant to aid those who wish to obtain fuller information than that which is given in this volume. Since comprehensive monographs on various groups of Protozoa are widely scattered and ordinarily not easily accessible, the author has endeavored to provide for each group as complete an information as possible for general reference purpose within the limited space, and hopes that the present work has reference value for teachers of biology, field workers in pure and applied biological sciences, veterinarians, physicians, public health workers, laboratory technicians, and others.

The author is under obligation to numerous writers for their valuable contributions which have been incorporated in the text. Special thanks are due Professor L. R. Cleveland, Harvard University; Professor R. P. Hall, New York University; Professor H. Kirby, Jr., University of California; Professor L. E. Noland, University of Wisconsin; Professor H. J. Van Cleave, University of Illinois; Professor D. H. Wenrich, University of Pennsylvania; and Professor L. L. Woodruff, Yale University, for their valued criticisms and suggestions. The author further wishes to express his appreciation to Mr. Charles C Thomas, for his patient and kind cooperation which has aided greatly in the completion and appearance of the present work.

R.R.K.

Urbana, Illinois, U.S.A.
July, 1939

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PROTOZOOLOGY

CHAPTER 1

Introduction

PROTOZOA are unicellular animals. The body of a protozoan is morphologically a single cell and manifests all characteristics common to the living thing. The various activities which make up the phenomena of life are carried on by parts within the body or cell. These parts are comparable with the organs of a metazoan which are composed of a large number of cells grouped into tissues and are called **organellae** or cell-organs. Thus one sees that the one-celled protozoan is a complete organism somewhat unlike the cell of a metazoan, each of which is dependent upon other cells and cannot live independently. From this viewpoint, certain students of protozoology maintain that the Protozoa are non-cellular, and not unicellular, organisms. Dobell (1911) for example, points out that the "cell" is employed to designate 1) the whole protozoan body, 2) a part of an organism and, 3) a potential whole organism (a fertilized egg) which consequently resulted in a confused state of knowledge regarding living things, and, therefore, proposed to define a cell as a mass of protoplasm composing part of an organism, and further considered that the protozoan is a non-cellular but complete organism, differently organized as compared with cellular organisms, the Metazoa and Metaphyta. The great majority of protozoologists, however, continue to consider the Protozoa as unicellular animals. Through the processes of organic evolution, they have undergone cytological differentiation and the Metazoa histological differentiation.

In being unicellular, the Protozoa and the Protophyta are alike. The majority of the Protozoa are quite clearly distinguishable from the majority of the Protophyta on the basis of nuclear condition, method of nutrition, direction of division-plane, etc. While numerous Protophyta appear to possess scattered nuclear material or none at all, the Protozoa contain at least one nucleus. It is generally considered that the binary fission of the Protozoa and the Protophyta is longitudinal and transverse, respectively. A great majority of Ciliata, however, multiply by transverse division. In general the nutrition of Protozoa is holo-

zoic and of Protophyta, holophytic; but there are large numbers of Protozoa which nourish themselves by holophytic method. Thus an absolute and clean-cut separation of the two groups of unicellular organisms is not possible. Haeckel coined the name **Protista** to include these organisms in a single group, but this is not generally adopted, since it includes undoubted animals and plants, thus creating an equal amount of confusion between it and the animal or the plant. Recently Calkins (1933) excluded chromatophore-bearing Mastigophora from his treatment of Protozoa, thus placing organisms similar in every way, except the presence or absence of chromatophores, in two different groups. This intermingling of characteristics between the two groups of microorganisms shows clearly their close interrelationship and suggests strongly their common ancestry.

Although the majority of Protozoa are solitary and the body is composed of a single cell, there are a few forms in which the body is made up of more than one cell. These forms, which are called colonial Protozoa, are well represented by the members of Phytomastigina, in which the individuals are either joined by cytoplasmic threads or embedded in a common matrix. These cells are alike both in structure and in function, although in several genera there may be differentiation of the individuals into reproductive and vegetative cells. Unlike the cells in a metazoan which form tissues, these vegetative cells of colonial Protozoa are not dependent upon other cells; therefore, they do not form any tissue. The reproductive cells produce zygotes through sexual fusion, which subsequently undergo repeated division and may produce a stage comparable with the blastula stage of a metazoan, but never reaching the gastrula stage. Thus colonial Protozoa are only cell-aggregates without histological differentiation and may thus be distinguished from the Metazoa.

Between 15,000 and 20,000 species of Protozoa are known to man. From comparatively simple forms such as *Amoeba*, up to highly complicated organisms as represented by numerous ciliates, the Protozoa vary exceedingly in their body organization, morphological characteristics, behavior, habitat, etc., which necessitates a taxonomic arrangement for proper consideration as set forth in detail in chapters 7 to 43.

Relationship of protozoology to other fields of biological science

A brief consideration of the relationship of Protozoology to other fields of biology and its possible applications may not be out of place here. Since the Protozoa are single-celled animals manifesting the characteristics common to all living things, they have been studied by numerous investigators with a view to discovering the nature and mechanism of various phenomena, the sum-total of which is known collectively as life. Though the investigators generally have been disappointed in the results, inasmuch as the assumed simplicity of unicellular organisms has proved to be offset by the complexity of their cell-structure, nevertheless any discussion of biological principles today must take into account the information obtained from studies of Protozoa. It is now commonly recognized that adequate information on various types of Protozoa is a prerequisite to a thorough comprehension of biology and to proper application of biological principles.

Practically all students agree in holding that the higher types of animals have been derived from organisms which existed in the remote past and which probably were somewhat similar to the Protozoa of the present day. Since there is no sharp distinction between the Protozoa and the Protophyta or between the Protozoa and the Metazoa, and since there are intermediate forms between the major classes of the Protozoa themselves, progress in protozoology contributes toward the advancement of our knowledge of the steps by which living things in general evolved.

Geneticists have undertaken studies on heredity and variation among Protozoa. "Unicellular animals," wrote Jennings (1909), "present all the problems of heredity and variation in miniature. The struggle for existence in a fauna of untold thousands showing as much variety of form and function as any higher group, works itself out, with ultimate survival of the fittest, in a few days under our eyes, in a finger bowl. For studying heredity and variation we get a generation a day, and we may keep unlimited numbers of pedigreed stock in a watch glass that can be placed under the microscope." Morphological variations are encountered commonly in all forms. Whether variation is due to germinal or environmental conditions, is often difficult to determine. The recent discovery of the sex reaction types in *Paramecium aurelia* (Son-

neborn; Kimbell) and in *P. bursaria* (Jennings) will probably assist in bringing to light many genetic problems of Protozoa which have remained obscure in the past.

Parasitic Protozoa are limited to one or more specific hosts. Through studies of the forms belonging to one and the same genus or species, the phylogenetic relation among the host animals may be established or verified. The mosquitoes belonging to the genera *Culex* and *Anopheles*, for instance, are known to transmit avian and human *Plasmodium* respectively. They are further infected by specific microsporidian parasites. For instance, *Thelohania legeri* has been found widely in many species of anopheline mosquitoes only; *T. opacita* has, on the other hand, been found in culicine mosquitoes, although the larvae of the species belonging to these two genera live frequently in the same body of water. By observing certain intestinal Protozoa in some monkeys, Hegner obtained evidence of the probable phylogenetic relationship between them and other higher mammals. The relation of various Protozoa of the wood-roach to those of the termite, as revealed by Cleveland and his associates, gives further proof that the Blattidae and the Isoptera are of the common origin.

Study of a particular group of parasitic Protozoa and their hosts may throw light on the geographic condition of the earth in the remote past. The members of the genus *Zelleriella* are usually found in the colon of the frogs belonging to the family Leptodactylidae. Through an extensive study of these amphibians from South America and Australia, Metcalf found that the species of *Zelleriella* occurring in the frogs of the two continents are almost identical. He finds it more difficult to conceive of convergent or parallel evolution of both the hosts and the parasites, than to assume that there once existed between Patagonia and Australia a land connection over which frogs, containing *Zelleriella*, migrated.

Experimental studies of large Protozoa have thrown light on the relation between the nucleus and the cytoplasm, and have furnished a basis for an understanding of regeneration in animals. In Protozoa we find various gradations of nuclear division ranging from a simple amitotic division to a complex process comparable in every detail with the typical metazoan mitosis, so that a great part of our knowledge of cytology is based upon studies of protozoan cells.

Through the studies of various investigators in the past forty years, it has now become known that numerous parasitic Protozoa occur in man. *Entamoeba histolytica*, *Balantidium coli*, and three species of *Plasmodium*, all of which are pathogenic to man, are widely distributed throughout the world. In certain restricted areas are found other pathogenic forms, such as *Trypanosoma* and *Leishmania*. Since all parasitic Protozoa presumably have originated in free-living forms and since our knowledge of the morphology, physiology and reproduction of the parasitic forms has largely been obtained through studies of the free-living organisms, a general knowledge of the entire phylum is necessary to understand the parasitic forms.

Recent studies have further revealed that almost all domestic animals are hosts to numerous parasitic Protozoa, many of which are responsible for serious infectious diseases. Many of the forms found in domestic animals are morphologically indistinguishable from those occurring in man. *Balantidium coli* is now generally considered as a parasite of swine, and man is its secondary host. Knowledge of protozoan parasites is useful to medical practitioners, just as it is essential to veterinarians inasmuch as certain diseases in animals, such as Texas fever, dourine, nagana, black-head, coccidiosis, etc., are caused by protozoans.

Sanitary betterment and improvement are fundamental requirements in the modern civilized world. One of man's necessities is safe drinking water. The majority of Protozoa live freely in various bodies of water and some of them seem to be responsible, if present in sufficiently large numbers, for giving certain odors to the waters of reservoirs or ponds (p. 95). But these Protozoa which are occasionally harmful are relatively small in number compared with those which are beneficial to man. It is generally understood that bacteria feed on various waste materials present in polluted water, but that upon reaching a certain population, they would cease to multiply and would allow the excess organic substances to undergo decomposition. Numerous holozoic Protozoa, however, feed on the bacteria and prevent them from reaching the saturation population. Protozoa thus seem to help indirectly in the purification of the water. Protozoology therefore must be considered as an important part of modern sanitary science.

Young fish feed extensively on small aquatic organisms, such

as larvae of insects, small crustaceans, annelids, etc., all of which depend largely upon Protozoa and Protophyta as sources of food supply. Thus the fish are indirectly dependent upon Protozoa as food material. On the other hand, there are numbers of Protozoa which live at the expense of fish. The Myxosporidia are almost exclusively parasites of fish and often cause death to large numbers of commercially important fishes. Success in fish-culture, therefore, requires among other things a thorough knowledge of Protozoa.

Since Russel and Hutchinson suggested some thirty years ago that Protozoa are probably a cause of limitation of the numbers, and therefore the activities of bacteria in the soil and thus tend to decrease the amount of nitrogen which is given to the soil by the nitrifying bacteria, several investigators have brought out the fact that in the soils of temperate climates Protozoa are present commonly and active throughout the year. The exact relation between specific protozoans and bacteria in the soil is a matter which still awaits future investigations, although numerous experiments and observations have already been made. All soil investigators should be acquainted with the biology and taxonomy of free-living protozoans.

It is a matter of common knowledge that the silkworm and the honey bee suffer from protozoan infection known as microsporidiosis. Sericulture in southern Europe suffered great damages in the middle of the nineteenth century because of the "pébrine" disease, caused by the microsporidian, *Nosema bombycis*. During the first decade of the present century, another microsporidian, *Nosema apis*, was found to destroy a large number of honey bees. Methods of control have been developed and put into practice so that these microsporidian infections are at present not serious, even though they still occur. On the other hand, other Microsporidia are now known to infect certain insects, such as mosquitoes and lepidopterous pests, which, when heavily infected, die sooner or later. Methods of destruction of these insects by means of chemicals are more and more used, but attention should also be given to utilization of the parasitic Protozoa and Protophyta for this purpose.

While the majority of Protozoa lack permanent skeletal structures and their fossil forms are unknown, there are at least two large groups in the Sarcodina which possess conspicuous shells

and which are found as fossils. They are Foraminifera and Radiolaria. From early palaeozoic times down to the present day, the carbonate of lime which makes up the skeletons of numerous Foraminifera has been left embedded in various rock strata. Although there is no distinctive foraminiferan fauna characteristic of a given geologic period, there are certain peculiarities of fossil Foraminifera which distinguish one formation from the other. From this fact one can understand that knowledge of foraminiferous rocks is highly useful in checking up logs in well drilling. The skeletons of the Radiolaria are the main constituent of the ooze of littoral and deep-sea regions. They have been found abundantly in siliceous rocks of the palaeozoic and the mesozoic, and are also identified with the clays and other formations of the miocene. Thus knowledge of these two orders of Sarcodina, at least, is essential for the student of geology and paleontology.

The history of protozoology

Aside from a comparatively small number of large forms, Protozoa are unobservable with the naked eye, so that we can easily understand why they were unknown prior to the invention of the microscope. Antony van Leeuwenhoek (1632–1723) is commonly recognized as the father of protozoology. Grinding lenses himself, Leeuwenhoek made more than four hundred microscopes, including one which, it is said, had a magnification of 270 times (Harting). Among the many things he discovered were various Protozoa. According to Dobell (1932), Leeuwenhoek saw for the first time in history, free-living Protozoa in fresh water in 1674. Among them, he observed bodies “green in the middle, and before and behind white,” which Dobell interprets were *Euglena*. Between 1674 and 1716 he apparently observed numerous microscopic organisms which he communicated to the Royal Society of London and which, as Dobell considered, were *Vorticella*, *Stylonychia*, *Carchesium*, *Volvox*, *Haematococcus*, *Coleps*, *Kerona*, *Anthophysa*, *Elphidium*, *Polytoma*, etc. According to Dobell, Huygens gave in 1678 “unmistakable descriptions of *Chilodon*(ella), *Paramecium*, *Astasia* and *Vorticella*, all found in infusions.”

Colpoda was seen by Bouonanni (1691) and Harris (1696) re-discovered *Euglena*. In 1718 there appeared the first treatise on microscopic organisms, particularly of Protozoa, by Joblot who emphasized the non-existence of abiogenesis by using boiled hay-

infusions in which no Infusoria developed without exposure to the atmosphere. This experiment confirmed that of Redi who, twenty years before, had made his well-known experiments by excluding flies from meat. Joblot illustrated, according to Woodruff (1937), Paramecium, the slipper animalcule, with the first identifiable figure. Trembly (1715) studied division in some ciliates, including probably Paramecium, which generic name was coined by Hill in 1752. Noctiluca was first described by Baker (1753).

Rösel (1755) observed an amoeba, possibly *Amoeba proteus* or an allied form, which he called "der kleine Proteus," and also Vorticella, Stentor, and Volvox. Ledermüller is said to have coined the term "Infusoria" in 1763 (Bütschli). By using the juice of geranium, Ellis (1770) caused the extrusion of the 'fins' (trichocysts) in Paramecium. Eichhorn (1783) observed the heliozoan, Actinosphaerium, which now bears his name. O. F. Müller described Ceratium a little later and published two works on the Infusoria (1786). Although he included unavoidably some Metazoa and Protophyta in his monographs, some of his descriptions and figures of Ciliata were so well done that they are of value even at the present time.

At the beginning of the nineteenth century the cyclosis in Paramecium was brought to light by Gruithuisen. Goldfuss (1817) coined the term "**Protozoa**," including in it the coelenterates. Ten years later there appeared d'Orbigny's systematic study of the Foraminifera, which he considered as microscopical cephalopods. In 1828 Ehrenberg began publishing his observations on Protozoa and 1838 he summarized his contributions in *Die Infusionsthierchen als vollkommene Organismen*, in which he diagnosed genera and species so well that many of them still hold good. Ehrenberg excluded Rotatoria and Cercaria from Infusoria. Through the studies of Ehrenberg the number of known Protozoa increased greatly; he, however, proposed the term "Polygastricha," under which he placed Mastigophora, Rhizopoda, Ciliata, Suctoria, desmids, etc., since he believed that the food vacuoles present in them were stomachs. This hypothesis became immediately the center of controversy, which incidentally, together with the then-propounded cell theory and improvements in microscopy, stimulated researches on Protozoa.

Dujardin (1835) took pains in studying the protoplasm of various Protozoa and found it alike in all. He named it "sarcode."

In 1841 he published an extensive monograph of various Protozoa which came under his observations. The term "Rhizopoda" was coined by this investigator. The commonly used term "protoplasm" was coined by Purkinje in 1840. The Protozoa was given a distinct definition by Siebold in 1845, as follows: "Die Thiere, in welchen die verschiedenen Systeme der Organe nicht scharf ausgeschieden sind, und deren unregelmässige Form und einfache Organization sich auf eine Zelle reduzieren lassen." Siebold subdivided Protozoa into Infusoria and Rhizopoda. The sharp differentiation of Protozoa as a group certainly inspired numerous microscopists. As a result, various students brought forward several group names, such as Radiolaria (J. Müller, 1858), Ciliata (Perty, 1852), Flagellata (Cohn, 1853), Suctoria (Claparède and Lachmann, 1858), Heliozoa, Protista (Haeckel, 1862, 1866), Mastigophora (Diesing, 1865), etc. Of Suctoria, Stein failed to see the real nature (1849), but his two monographs on Ciliata and Mastigophora (1854, 1859–1883) contain concise descriptions and excellent illustrations of numerous species. Haeckel (1873), who went a step further than Siebold by distinguishing between Protozoa and Metazoa, devoted ten years to his study of Radiolaria, especially those of the Challenger collection, and described in his celebrated monographs more than 4000 species.

In 1879 the first comprehensive monograph on the Protozoa of North America was put forward by Leidy under the title of *Freshwater Rhizopods of North America*, which showed the wide distribution of many known forms of Europe and revealed a number of new and interesting forms. This work was followed by Stokes' *The freshwater Infusoria of the United States*, which appeared in 1888. Bütschli (1880–1889) established Sarcodina and made an excellent contribution to the taxonomy of the then-known species of Protozoa, which is still considered as one of the most important works on general protozoology. The painstaking researches by Maupas, on the conjugation of ciliates, corrected erroneous interpretation of the phenomenon observed by Balbiani some thirty years before and gave impetus to a renewed cytological study of Protozoa. The variety in form and structure of the protozoan nuclei became the subject of intensive studies by several cytologists. Weismann (1881) put into words the immortality of the Protozoa. Schaudinn contributed much toward the cytological and developmental studies of Protozoa.

In the first year of the present century, Calkins in the United States and Doflein in Germany wrote modern textbooks on protozoology dealing with the biology as well as the taxonomy. Calkins initiated the so-called isolation pedigree culture of ciliates in order to study the physiology of conjugation and other phenomena connected with the life-history of the ciliates. The application of this method has been found very popular in recent years.

Today the Protozoa are more and more intensively and extensively studied from both the biological and the parasitological sides, and important contributions appear continuously. Since all parasitic Protozoa appear to have originated in free-living forms, the comprehension of the morphology, physiology, and development of the latter group obviously is fundamentally important for a thorough understanding of the former group.

Compared with the advancement of our knowledge on free-living Protozoa, that on parasitic forms has been very slow. This is to be expected, of course, since the vast majority of them are so minute that the discovery of their presence has been made possible only through improvements in the microscope and in technique.

Here again Leeuwenhoek seems to have been the first to observe a parasitic protozoan, for he observed, according to Dobell, in the fall of 1674, the oocysts of the coccidian, *Eimeria stiedae*, in the contents of the gall bladder of an old rabbit; in 1681, *Giardia intestinalis* in his own diarrhœic stools; and in 1683, *Opalina* and *Nyetotherus* in the gut contents of frogs. There is no record of anyone having seen Protozoa living in other organisms until 1828, when Dufour's account of the gregarine from the intestine of coleopterous insects appeared. Some ten years later, Hake rediscovered the oocysts of *Eimeria stiedae*. A flagellate was observed in the blood of salmon by Valentin in 1841, and the frog trypanosome was discovered by Gluge and Gruby (1842), the latter author creating the genus *Trypanosoma* for it.

The gregarines were a little later given attention by Siebold (1839), Kölliker (1848) and Stein (1848). The year 1849 marks the first record of an amoeba being found in man, for Gros then observed *Entamoeba gingivalis* in the human mouth. Five years later, Davaine found in the stools of cholera patients two flagellates (*Trichomonas* and *Chilomastix*). Kloss in 1855 observed the

coccidian, *Klossia helicina*, in the excretory organ of *Helix* and Eimer (1870) made an extensive study of *Coccidia* occurring in various animals. *Balantidium coli* was discovered by Malmsten in 1857. Lewis in 1870 observed *Entamoeba coli* in India, and Lösch in 1875 found *Entamoeba histolytica* in Russia. At the beginning of the last century, an epidemic disease, pébrine, of the silkworm appeared in Italy and France, and a number of biologists became engaged in its investigation. Foremost of all, Pasteur (1870) made an extensive report on the nature of the causative organism, now known as *Nosema bombycis*, and also on the method of control and prevention. Perhaps this is the first scientific study of a parasitic protozoan to result in an effective practical method of control of its infection.

Lewis observed in 1878 an organism which is since known as *Trypanosoma lewisi* in the blood of rats. In 1879 Leuckart created the group "Sporozoa," including in it the gregarines and coccidians. The groups under Sporozoa were soon definitely designated. They are Myxosporidia (Bütschli, 1881), Microsporidia (Balbiani, 1882) and Sarcosporidia (Balbiani, 1882).

Parasitic protozoology received a far-reaching stimulus when Laveran (1880) discovered the malarial parasite in the human blood. Smith and Kilborne (1893) demonstrated that the *Babesia* of the Texas fever of cattle in the southern United States was transmitted by cattle ticks from host to host, and thus brought to light for the first time the close relationship which exists between an arthropod and a parasitic protozoan. Two years later, Bruce discovered *Trypanosoma brucei* in the blood of horses and cattle suffering from "nagana" disease in Africa, and in the following year he showed by experiments that the tsetse fly transmits the trypanosome from host to host. Studies of malarial diseases continued and several important contributions appeared. Golgi (1886, 1889) studied the schizogony and its relation to the occurrence of fever and was able to distinguish two types of fever. MacCallum (1897-1898) found in the United States the union of a microgamete and a macrogamete of *Haemoproteus* of birds. Almost at the same time, Schaudinn and Siedlecki (1897) showed that anisogamy results in the production of zygotes in *Coccidia*. The latter author published later correct observations on the life-cycle of *Coccidia* (1898, 1899).

Ross (1898) showed how *Plasmodium praecox* was carried by

Culex fatigans and described its life-cycle. Since that time several investigators have brought to light important observations concerning the biology and development of these organisms and their relation to man. In the present century, Forde and Dutton (1901) observed that the sleeping sickness in Africa is due to an infection by *Trypanosoma gambiense*. In 1903 Leishman and Donovan recognized *Leishmania* of "kala-azar."

Artificial cultivation of bacteria had contributed toward a very rapid advancement in bacteriology, and it was natural, as the number of known parasitic Protozoa rapidly increased, that attempts to cultivate them in vitro should be made. Musgrave and Clegg (1904) cultivated, on bouillon-agar, small free-living amoebae from old fecal matter. In 1905 Novy and McNeal cultivated successfully the trypanosome of birds in blood-agar medium, which remained free from bacterial contamination and in which the organisms underwent multiplication. Almost all species of *Trypanosoma* and *Leishmania* have since been cultivated in a similar manner. This serves for detection of a mild infection and also identification of the species involved. It was found, further, that the changes which these organisms underwent in the culture media were imitative of those that took place in the invertebrate host, thus contributing toward the life-cycle studies of them.

Bass (1911), and Bass and Johns (1912) demonstrated that *Plasmodium* of man could be cultivated in vitro for a few generations. During and since the World War, it became known that numerous intestinal Protozoa of man are widely present throughout the tropical, subtropical and temperate zones. Taxonomic, morphological and developmental studies on these forms have therefore appeared in an enormous number. Cutler (1918) seems to have succeeded in cultivating *Entamoeba histolytica*, though his experiment was not repeated by others. Barret and Yarborough (1921) cultivated *Balantidium coli* and Boeck (1921) also cultivated *Chilomastix mesnili*. Boeck and Drbohlav (1925) succeeded in cultivating *Entamoeba histolytica*, and their work was repeated and improved upon by several investigators. While the cultivation has not yet thrown much light on this and similar amoebae, it reveals certain evidences that there is no sexual reproduction in these amoebae. Since that time, almost all intestinal Protozoa of both vertebrates and invertebrates have been cultivated by numerous investigators.

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CHAPTER 2

Ecology

WITH regard to their habitats, the Protozoa may be divided into free-living forms and those living on (epizoic) or in (endozoic) other organisms.

The free-living Protozoa

The vegetative or trophic stage of free-living Protozoa have been found in every type of fresh and salt water, soil and decaying organic matter. In the circumpolar regions or at extremely high altitudes, certain Protozoa occur at times in fairly large numbers. The factors, which influence their distribution in a given body of water, are temperature, light, chemical composition, acidity, kind and amount of food, and degree of adaptability of the individual protozoans to various environmental changes. Their early appearance as living organisms, their adaptability to various habitats and their capacity to remain viable in encysted condition possibly account for the wide distribution of the Protozoa throughout the world. The common free-living amoebae, numerous testaceans and others, to mention a few, of fresh waters, have been observed in innumerable parts of the world.

Temperature. The majority of Protozoa are able to live only within a small range of temperature variation, although in the encysted state they can withstand a far greater temperature fluctuation. The lower limit of the temperature is marked by the freezing of the protoplasm, and the upper limit by the destructive chemical change within the body. The temperature toleration seems to vary among different species of Protozoa; and even in the same species under different conditions. For example, Chalkley (1930) placed *Paramecium caudatum* in 4 culture media (balanced saline, saline with potassium excess, saline with calcium excess, and saline with sodium excess), all with pH from 5.8 or 6 to 8.4 or 8.6, at 40°C. for 2–16 minutes and found that 1) the resistance varies with the hydrogen-ion concentration, maxima appearing in the alkaline and acid ranges, and a minimum at or near about 7.0; 2) in a balanced saline, and in saline with an excess of sodium or potassium, the alkaline maximum is the higher, while

in saline with an excess of calcium, the acid maximum is the higher; 3) in general acidity decreases and alkalinity increases resistance; and 4) between pH 6.6 and 7.6, excess of potassium decreases resistance and excess of calcium increases resistance. Glaser and Coria (1933) cultivated *Paramecium caudatum* on dead yeast free from living organisms at 20–28°C. (optimum 25°C.) and noted that at 30°C. the organisms were killed. Doudoroff (1936), on the other hand, found that in *P. multimicronucleata* its resistance to raised temperature was low in the presence of food, but rose to a maximum when the food was exhausted, and there was no appreciable difference in the resistance between single and conjugating individuals.

The thermal waters of hot springs have been known to contain living organisms including Protozoa. Glaser and Coria obtained from the thermal springs of Virginia, several species of Mastigophora, Ciliata, and an amoeba which were living in the water, the temperature of which was 34–36°C., but did not notice any protozoan in the water which showed 39–41°C. Uyemura and his co-workers made a series of studies on Protozoa living in various thermal waters of Japan, and reported that many species lived at unexpectedly high temperatures. Some of the Protozoa observed and the temperatures of the water in which they were found are as follows: *Amoeba* sp., *Vahlkampfia limax*, *A. radiosa*, 30–51°C.; *Amoeba verrucosa*, *Chilodonella* sp., *Lionotus fasciola*, *Paramecium caudatum*, 36–40°C.; *Oxytricha fallax*, 30–56°C.

Under experimental conditions, it has been shown repeatedly that many protozoans become accustomed to a very high temperature if the change be made gradually. Dallinger and Drysdale showed a long time ago that *Tetramitus rostratus* and two other species of flagellates could be cultivated in temperatures ranging from 16° to 70°C. In nature, however, the thermal death point of most of the free-living Protozoa appears to lie between 36° and 40°C. and the optimum temperature, between 16° and 25°C.

On the other hand, the low temperature seems to be less detrimental to Protozoa than the higher ones. Many protozoans have been found to live in water under ice, and several haematochrome-bearing Phytomastigina undergo vigorous multiplication on snow in high altitudes, producing the so-called "red snow." Efimoff (1924) demonstrated that *Paramecium*, *Frontonia*, *Colpidium* and other ciliates die quickly at –4°C., but by a quick and short

overcooling (not lower than $-9^{\circ}\text{C}.$) no injury is brought about. At $0^{\circ}\text{C}.$, *Paramecium* was able to multiply once in about 13 days. Wolfson (1935) studied *Paramecium* sp. in gradually descending subzero-temperature, and observed that as the temperature decreases the organisms often swim backward, its bodily movements cease and its cilia finally stop beating. If the low temperature exposure has not been of sufficient intensity or duration, warming induces a resumption of movement. Kept for 10–15 minutes at $10^{\circ}\text{C}.$, the organism increases its body volume and becomes rounded, from which condition it may recover if the temperature rises, but which otherwise is followed rapidly by a complete disintegration. When the water in which the ciliates are kept freezes, the organisms do not survive.

Light. In the *Phytomastigina* which include chromatophore-bearing flagellates, the sun light is essential to photosynthesis (p. 92). The sun light further plays an important rôle in those protozoans which are dependent upon chromatophore-possessing organisms as chief source of food supply. Hence the light is another factor concerned with the distribution of free-living protozoans in the water.

Chemical composition of water. The chemical nature of the water is another important factor which influences the very existence of Protozoa in a given body of water. Different Protozoa show different morphological as well as physiological characteristics. As numerous cultural experiments indicate that individual protozoan species requires a certain chemical composition of the water in which it is cultivated under experimental conditions, although this may be more or less variable among different forms (Needham et al.).

In their "biological analysis of water" Kolkwitz and Marsson (1908, 1909) distinguished four types of habitats for many aquatic plant, and a few animal, organisms, which were based upon the kind and amount of inorganic and organic matter and amount of oxygen present in the water: namely, *katharobic*, *oligosaprobic*, *mesosaprobic*, and *polysaprobic*. **Katharobic** protozoans are those which live in mountain springs, brooks, or ponds, the water of which is rich in oxygen, but free from organic matter. **Oligosaprobic** forms are those that inhabit waters which are rich in mineral matter, but in which no purification processes are taking place. Many *Phytomastigina*, various testaceans and many cili-

ates, such as *Frontonia*, *Laecymaria*, *Oxytricha*, *Stylonychia*, *Vorticella*, etc., inhabit such waters. **Mesosaprobic** protozoans live in waters in which active oxidation and decomposition of organic matter are taking place. The majority of freshwater protozoans belong to this group: namely, numerous *Phytomastigina*, *Heliozoa*, *Zoomastigina*, and all orders of *Ciliata*. Finally **poly-saprobic** forms are capable of living in waters which, because of dominance of reduction and cleavage processes of organic matter, contain at most a very small amount of oxygen and are rich in carbonic acid gas and nitrogenous decomposition products. The black bottom slime contains usually an abundance of ferrous sulphide and other sulphurous substances. Lauterborn (1901) called this *sapropelic*. Examples of polysaprobic protozoans are *Pelomyxa palustris*, *Euglypha alveolata*, *Pamphagus armatus*, *Mastigamoeba*, *Trepomonas agilis*, *Hexamita inflata*, *Rhynchomonas nasuta*, *Heteronema acus*, *Bodo*, *Cercomonas*, *Dactylochlamys*, *Ctenostomata*, etc. The so-called "sewage organisms" abound in such habitat (Lackey).

Certain free-living Protozoa which inhabit waters rich in decomposing organic matter are frequently found in the fecal matter of various animals. Their cysts either pass through the alimentary canal of the animal unharmed or are introduced after the feces are voided, and undergo development and multiplication in the fecal infusion. Such forms are collectively called **coprozoic** Protozoa. The coprozoic protozoans grow easily in suspension of old fecal matter which are rich in decomposed organic matter and thus show a strikingly strong capacity of adapting themselves to conditions different from those of the water in which they normally live. Some of the Protozoa which have been referred to as coprozoic and which are mentioned in the present work are, as follows: *Scytomonas pusilla*, *Rhynchomonas nasuta*, *Cercomonas longicauda*, *C. crassicauda*, *Trepomonas agilis*, *Dimastigamoeba gruberi*, *Hartmanella hyalina*, *Chlamydomphrys stercorea* and *Tillina magna*.

As a rule, the presence of sodium chloride in the sea water prevents the occurrence of the large number of fresh-water inhabitants. Certain species, however, have been known to live in both fresh and brackish or salt water. Among the species mentioned in the present work, the following species have been reported to occur in both fresh and salt waters: *Mastigophora*: *Amphidinium*

lacustris, *Ceratium hirundinella*; Sarcodina: *Lieberkuhnia wagneri*; Ciliata: *Mesodinium pulex*, *Prorodon discolor*, *Lacrymaria olor*, *Amphileptus claparedei*, *Lionotus fasciola*, *Nassula aurea*, *Trochiloides recta*, *Chilodonella cucullulus*, *Trimyema compressum*, *Paramecium calkinsi*, *Colpidium campylum*, *Platynematum sociale*, *Cinetochilum margaritaceum*, *Pleuronema coronatum*, *Caenomorpha medusula*, *Spirostomum minus*, *S. teres*, *Climacostomum virens*, and *Thuricola folliculata*; Suctoria: *Metacineta mystacina*, *Endosphaera engelmanni*.

It seems probable that many other protozoans are able to live in both fresh and salt water, judging from the observations such as that made by Finley (1930) who subjected some fifty species of freshwater Protozoa of Wisconsin to various concentrations of sea water, either by direct transfer or by gradual addition of the sea water. He found that *Bodo uncinatus*, *Uronema marina*, *Pleuronema jaculans* and *Colpoda aspera* are able to live and reproduce even when directly transferred to sea water, that *Amoeba verrucosa*, *Euglena*, *Phacus*, *Monas*, *Cyclidium*, *Euplotes*, *Lionotus*, *Paramecium*, *Stylonychia*, etc., tolerate only a low salinity when directly transferred, but, if the salinity is gradually increased, they live in 100 per cent sea water, and that *Arcella*, *Cyphoderia*, *Aspidisca*, *Blepharisma*, *Colpoda cucullus*, *Halteria*, etc., could not tolerate 10 per cent sea water even when the change was gradual. Finley noted no morphological changes in the experimental protozoans which might be attributed to the presence of the salt in the water, except *Amoeba verrucosa*, in which certain structural and physiological changes were observed as follows: as the salinity increased, the pulsation of the contractile vacuole became slower. The body activity continued up to 44 per cent sea water and the vacuole pulsated only once in 40 minutes, and after systol, it did not reappear for 10–15 minutes. The organism became less active above this concentration and in 84 per cent sea water the vacuole disappeared, but there was still a tendency to form the characteristic ridges, even in 91 per cent sea water, in which the organism was less fan-shaped and the cytoplasm seemed to be more viscous. Yocom (1934) found that *Euplotes patella* was able to live normally and multiply up to 66 per cent of sea water; above that concentration no division was noticed, though the organism lived for a few days in up to 100 per cent salt water, and *Paramecium caudatum* and *Spirostomum ambigu-*

um were less adaptive to salt water, rarely living in 60 per cent sea water.

Hydrogen-ion concentration. Closely related to the chemical composition is the hydrogen-ion concentration (pH) of the water which influences the distribution of Protozoa. The hydrogen-ion concentration of freshwater bodies vary a great deal between highly acid bog waters in which various testaceans may frequently be present, to highly alkaline water in which such forms as *Acanthocystis*, *Hyalobryon*, etc., occur. In standing deep fresh water, the bottom region is often acid because of the decomposing organic matter, while the surface water is less acid or slightly alkaline due to the photosynthesis of green plants which utilize carbon dioxide. Several investigators have recently made observations on the pH range of the water or medium in which certain protozoans live, grow, and multiply, which data are collected in a table on page 22.

Seemingly various Protozoa require a definite pH value in order to carry on maximum metabolic activities. As a matter of fact, Pringsheim, Hall, Loefer, Johnson, and others, found that sodium acetate may increase or decrease the growth rate of various *Phytomastigina* subject to the hydrogen-ion concentration of the culture media.

Food. The kind and amount of food available in a given body of water also controls the distribution of Protozoa. The food is ordinarily one of the deciding factors of the number of Protozoa in a natural habitat. Species of *Paramecium* and many other holozoic protozoans cannot live in waters in which bacteria or minute protozoans do not occur. If other conditions are favorable, then the greater the number of food bacteria, the greater the number of these protozoans. *Didinium nasutum* feeds almost exclusively on *Paramecium*, hence it cannot live in the absence of the latter ciliate. Euryphagous protozoans are widely distributed and stenophagous forms are limited in their distribution.

Some protozoans inhabit soil of various types and localities. Under ordinary circumstances, they occur near the surface, their maximum abundance being found at a depth of about 10–12 cm. (Sandon, 1927). It is said that a very few protozoans occur in the subsoil. Here also one notices a very wide geographical distribution of apparently one and the same species. For example, Sandon found *Amoeba proteus* in samples of soil collected from Green-

Protozoa	pH range of medium in which growth occurs	Optimum range	Observers
In bacteria-free cultures			
<i>Euglena gracilis</i>	3.5-9.0	—	Dusi
	3.0-7.7	6.7	Alexander
	3.9-9.9	6.6	Jahn
<i>E. dcses</i>	6.5-8.0	7.0	Dusi
	5.3-8.0	7.0	Hall
<i>E. pisciformis</i>	6.0-8.0	6.5-7.5	Dusi
	5.4-7.5	6.8	Hall
<i>Chilomonas paramecium</i>	4.1-8.4	4.9; 7.0	Loefer
<i>Chlorogonium cuculorum</i>	4.8-8.7	7.1-7.5	Loefer
<i>C. elongatum</i>			
<i>Colpidium striatum</i>	4.0-8.9	5.5-5.7	Elliott
<i>C. campylum</i>	4.0-8.9	6.5	Elliott
<i>Glaucoma pyriformis</i>	4.0-8.9	4.8-5.3	Johnson
<i>G. ficaria</i>	4.0-9.5	5.1-6.0	Johnson
<i>Paramecium bursaria</i>	5.3-8.0	6.7-6.8	Loefer
In cultures containing bacteria			
<i>Carteria obtusa</i>	—	3.5-4.5	Wermel
<i>Acanthocystis aculeata</i>	7.4 or above	8.1	Stern
<i>Paramecium caudatum</i>	5.3-8.2	7.0	Darby
	6.0-9.5	7.0	Morea
<i>P. aurelia</i>	5.7-7.8	6.7	Morea
	5.9-8.2	—	Phelps
<i>P. multimicronucleata</i>	4.8-8.3	7.0	Jones
<i>P. sp.</i>	—	7.8-8.0	Saunders
	7.0-8.5	7.8-8.0	Pruthi
<i>Colpidium sp.</i>	6.0-8.5	—	Pruthi
<i>Colpoda cucullus</i>	5.5-9.5	6.5; 7.5	Morea
<i>Holophyra sp.</i>	6.5-7.4	—	Pruthi
<i>Plagiopyla sp.</i>	6.9-7.5	—	Pruthi
<i>Amphileptus sp.</i>	6.8-7.5	7.1-7.3	Pruthi
<i>Spirostomum ambiguum</i>	6.8-7.5	7.4	Saunders
<i>S. sp.</i>	6.5-8.0	7.5	Morea
<i>Blepharisma undulans</i>	—	6.5	Moore
<i>Gastrostyla sp.</i>	6.0-8.5	—	Pruthi
<i>Stylonychia pustulata</i>	6.0-8.0	6.7; 8.0	Darby

land, Tristan da Cunha, Gough Island, England, Mauritius, Africa, India, and Argentina. This amoeba is known to occur in various parts of North America, Europe, Japan, and Australia. The majority of Testacea inhabit moist soil in abundance. Sandon observed *Trinema enchelys* in the soils of Spitzbergen,

Greenland, England, Japan, Australia, St. Helena, Barbados, Mauritius, Africa, and Argentina.

The parasitic Protozoa

Some Protozoa belonging to all groups live on or in other organisms. The Sporozoa are made up exclusively of such forms. The relationships between the host and the protozoan differ in various ways, which make the basis for distinguishing the associations into three types as follows: **commensalism**, **symbiosis**, and **parasitism**.

The **commensalism** is an association in which an organism, the commensal, is benefited, while the host is neither injured nor benefited. Depending upon the location of the commensal in the host body, the ectocommensalism or endocommensalism is used. The ectocommensalism is often represented by Protozoa which may attach themselves to any aquatic animals that inhabit the same body of water, as shown by various species of Chonotricha, Peritricha, and Suctoria. In other cases, there is a definite relationship between the commensal and the host. For example, *Kerona polyporum* is found on various species of Hydra, and the ciliates placed in Thigmotricha (p. 560) are inseparably associated with certain species of the mussels.

The endocommensalism is often difficult to distinguish from the endoparasitism, since the effect of the presence of the commensal upon the host cannot be easily understood. On the whole, the protozoans which live in the lumen of the alimentary canal of the host may be looked upon as endocommensals. These protozoans use undoubtedly part of the food material which could be used by the host, but they do not invade the host tissue. As examples of endocommensals may be mentioned: *Endamoeba blattae*, *Lophomonas blattarum*, *L. striata*, *Nyctotherus ovalis*, etc., of the cockroach; *Entamoeba coli*, *Iodamoeba butschlii*, *Endolimax nana*, *Dientamoeba fragilis*, *Chilomastix mesnili*, *Giardia intestinalis*, etc., of the human intestine; numerous species of Proto-ciliata of Anura, etc. Because of the difficulties mentioned above, the term **parasitic Protozoa**, in its broad sense, includes the commensals also.

The **symbiosis** on the other hand is an association of two species of organisms which is of mutual benefit. The cryptomonads belonging to Chrysidella ("zooxanthellae") containing yellow or

brown chromatophores, which live in Foraminifera and Radiolaria, and certain algae belonging to *Chlorella* ("zoochlorellae") containing green chromatophores, which occur in some freshwater protozoans, such as *Paramecium bursaria*, *Stentor amethystinus*, etc., are looked upon as holding symbiotic relationship with the respective protozoan host. Several species of the highly interesting *Hypermastigina*, which are present commonly and abundantly in various species of the termite and the woodroach *Cryptocercus*, have been demonstrated by Cleveland to digest the cellulose material which makes up the bulk of wood-chips the host animals take in and to transform it into glycogenous substances which are used partly by the host insects. If deprived of these flagellates by being subjected to oxygen under pressure or to a high temperature, the termites lose the flagellates and die, even though the intestine is filled with wood-chips. If removed from the gut of the termite, the flagellates die. Thus the association here may be said to be an absolute symbiosis.

The **parasitism** is an association in which one organism (the parasite) lives at the expense of the other (the host). Here also ectoparasitism and endoparasitism occur, although the former is not commonly found. *Hydramoeba hydroxena* (p. 321) feeds on ectodermal cells of *Hydra* which, according to Reynolds and Looper, die on an average in 6.8 days as a result of the infection and the amoebae disappear in from 4 to 10 days if removed from a host *Hydra*. *Costia necatrix* (p. 264) often occurs in an enormous number, attached to various freshwater fishes especially in an aquarium, by piercing through the epidermal cells and appears to disturb the normal functions of the host tissue. *Ichthyophthirius multifiliis* (p. 504), another ectoparasite of freshwater fishes, goes further by completely burying themselves in the epidermis and feeds on the host's tissue cells and, not infrequently, contributes toward the cause of the death of the host fishes.

The endoparasites absorb by osmosis the vital body fluid, feed on the host cells or cell-fragments by pseudopodia or cytostome, or enter the host tissues or cells themselves, living on the cytoplasm or in some cases on the nucleus. Consequently they bring about abnormal or pathological conditions upon the host which often succumbs to the infection. Endoparasitic Protozoa of man are *Entamoeba histolytica*, *Balantidium coli*, species of *Plasmodium* and *Leishmania*, *Trypanosoma gambiense*, etc. The Sporozoa, as

was stated before, are without exception coelozoic, histozoic, or cytozoic parasites.

Because of their modes of living, the endoparasitic Protozoa cause certain morphological changes in the cells, tissues, or organs of the host. The active growth of *Entamoeba histolytica* in the glands of the colon of the victim, produces slightly raised nodules first which develop into abscesses and the ulcers formed by the rupture of abscesses, may reach 2 cm. or more in diameter, completely destroying the tissues of the colon wall. Similar pathological changes are also noticed in the case of infection by *Balantidium coli*. In *Leishmania donovani*, the victim shows an increase in number of the large macrophages and mononuclears and also an extreme enlargement of the spleen. *Trypanosoma cruzi* brings about the degeneration of the infected host cells and an abundance of leucocytes in the infected tissues, followed by an increase of fibrous tissue. *T. gambiense*, the causative organism of African sleeping sickness, causes enlargement of lymphatic glands and spleen, followed by changes in meninges and an increase of cerebro-spinal fluid. Its most characteristic changes are the thickening of the arterial coat and the round-celled infiltration around the blood vessels of the central nervous system. Von Brand's (1938) summary of the carbohydrate metabolism of the pathogenic trypanosomes tends to show that the sugar is only partially oxidized in the presence of oxygen and that the carbohydrate metabolism of the infected host is disturbed, as shown mainly by the unbalanced condition of the blood sugar, by lowering of the glycogen reserves, and by reduced ability to build glycogen from sugar. Malarial infection is invariably accompanied by an enormous enlargement of the spleen ("spleen index"); the blood becomes watery; the erythrocytes decrease in number; the leucocytes, subnormal; but mononuclear cells increase in number; pigment granules which are set free in the blood plasma at the time of merozoite-liberation are engulfed by leucocytes; and enlarged spleen contains large amount of pigments which are lodged in leucocytes and endothelial cells. In *Plasmodium falciparum*, the blood capillaries of brain, spleen and other viscera may completely be blocked by infected erythrocytes.

In Myxosporidia which are either histozoic or coelozoic parasites of fishes, the tissue cells that are in direct contact with highly

enlarged parasites, undergo various morphological changes. For example, the circular muscle fibers of the small intestine of *Pomoxis sparoides*, which surround *Myxobolus intestinalis*, a myxosporidian, become modified a great deal and turn about 90° from the original direction, due undoubtedly to the stimulation exercised by the myxosporidian parasite (Fig. 1, a). In the case of another myxosporidian, *Thelohanellus notatus*, the connective tissue cells of the host fish surrounding the protozoan body, trans-

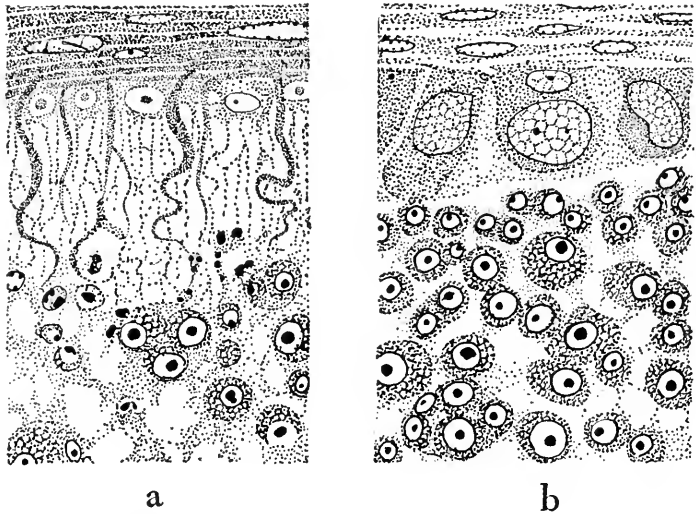


FIG. 1. Histological changes in host fish caused by myxosporidian infection, $\times 1920$ (Kudo). a, portion of a cyst of *Myxobolus intestinalis*, surrounded by peri-intestinal muscle of the black crappie; b, part of a cyst of *Thelohanellus notatus*, enveloped by the connective tissue of the blunt-nosed minnow.

form themselves into "epithelial cells" (Fig. 1, b), a state comparable to the formation of the ciliated epithelium from a layer of fibroblasts lining a cyst formed around a piece of ovary implanted into the adductor muscle of *Pecten* as observed by Drew (1911).

Practically all Microsporidia are cytozoic, and the infected cells become hypertrophied enormously, producing in one genus the so-called Glugea cysts (Fig. 220). In many cases, the hypertrophy of the nucleus of the infected cell is far more conspicuous than that of the cytoplasm (Fig. 218). Information concerning

toxic substances produced by parasitic Protozoa is meager. Sarcosporidia appear to produce a certain toxic substance which, when injected in the blood vessel, is highly toxic to experimental animals. This was named sarcocystine (Laveran and Mesnil) or sarcosporidiotoxin (Teichmann and Braun). As in bacterial infection, the reaction and resistance of the host to protozoan infection apparently differ among different individuals. Taliaferro demonstrated that there occur in the blood of animals suffering from trypanosomiasis or malaria, certain agents which would either inhibit the rate of multiplication of the parasites or destroy the parasites themselves.

With regard to the origin of parasitic Protozoa, it is generally agreed among biologists that the parasite in general evolved from the free-living form. The protozoan association with other organisms was begun when various protozoans which lived attached to, or by crawling on, submerged objects happened to transfer themselves to various invertebrates which occur in the same water. These Protozoa benefit by change in location as the host animal moves about, and thus enlarging the opportunity to obtain a continued supply of food material. Examples of such ectocommensals abound everywhere. The ectocommensalism may next lead into ectoparasitism as in the case of *Costia* or *Hydra-moeba*, and then again instead of confining themselves to the body surface, the Protozoa may bore into the body wall from outside and actually acquire the habit of feeding on tissue cells of the attached animals as in the case of *Ichthyophthirius*.

The next step in the evolution of parasitism must have been reached when Protozoa, accidentally or passively, were taken into the digestive system of the Metazoa. Such a sudden change in habitat appears to be fatal to most protozoans. But certain others possess extraordinary capacity to adapt themselves to an entirely different environment. For example, Dobell (1918) observed in the tad-pole gut, a typical free-living limax amoeba, with characteristic nucleus, contractile vacuoles, etc., which was found in numbers in the water containing the fecal matter of the tadpole. *Glaucoma pyriformis* (p. 548), a free-living ciliate, was found to occur in the body cavity of the larvae of *Thecobaldia annulata* (after MacArthur) and in the larvae of *Chironomus plumosus* (after Treillard and Lwoff). Lwoff successfully inoculated this ciliate into the larvae of *Galleria mellonella* which died

later from the infection. Recently Janda and Jírovec (1937) injected bacteria-free culture of this ciliate into annelids, molluses, crustaceans, insects, fishes, and amphibians, and found that only insects—all of 14 species (both larvae and adults)—became infected by this ciliate. In a few days after injection the haemocoel became filled with the ciliates. Of various organs, the ciliates were most abundantly found in the adipose tissue. The organisms were much larger than those present in the original culture. The insects, into which the ciliates were injected, died from the infection in a few days. The course of development of the ciliate within an experimental insect depended not only on the amount of the culture injected, but also on the temperature. At 1–4°C. the development was much slower than at 26°C.; but if an infected insect was kept at 32–36°C. for 0.5–3 hours, the ciliates were apparently killed and the insect continued to live. When *Glaucoma* taken from *Dixippus morosus* were placed in ordinary water, they continued to live and underwent multiplication. The ciliate showed a remarkable power of withstanding the artificial digestion; namely, at 18°C. they lived 4 days in artificial gastric juice with pH 4.2; 2–3 days in a juice with pH 3.6; and a few hours in a juice with pH 1.0. Cleveland (1928) observed *Trichomonas fecalis* in feces of a single human subject for three years which grew well in feces diluted with tap water, in hay infusions with or without free-living protozoans or in tap water with tissues at –3° to 37°C., and which, when fed *per os*, was able to live indefinitely in the gut of frogs and tadpoles. Reynolds (1936) found that *Colpoda steini*, a free-living ciliate of fresh water, occurs naturally in the intestine and other viscera of the land slug, *Agriolimax agrestis*, the slug forms being much larger than the free-living individuals.

It may further be speculated that Vahlkampfia, Hydramoeba, Schizamoebea, and Endamoeba, are the different stages of the course the intestinal amoebae might have taken during their evolution. Obviously endocommensalism in the alimentary canal was the initial phase of endoparasitism. When these endocommensals began to consume an excessive amount of food or to feed on the tissue cells of the host gut, they became the true endoparasites. Destroying or penetrating through the intestinal wall, they became first established in body cavities or organ cavities and then invaded tissues, cells or even nuclei, thus developing

into pathogenic Protozoa. The endoparasites developing in invertebrates which feed upon the blood of vertebrates as source of food supply, will have opportunities to establish themselves in the higher animals.

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CHAPTER 3

Morphology

PROTOZOA range in size from ultramicroscopic to macroscopic, though they are on the whole minute microscopic animals. The parasitic forms, especially cytozoic parasites, are often extremely small, while free-living protozoans are usually of much larger dimensions. Noctiluca, Foraminifera, Radiolaria, many ciliates such as Stentor, Bursaria, etc., represent larger forms. Colonial protozoans such as Carchesium, Zoothamnium, Ophrydium, etc., are even greater than the solitary forms. Plasmodium, Leishmania, and microsporidian spores may be mentioned as examples of the smallest forms. The unit of measurement employed in protozoology is, as in general microscopy, 1 micron (μ) which is equal to 0.001 mm.

The body forms of Protozoa are even more varied, and frequently, because of its extreme plasticity it does not remain constant. From a small simple spheroidal mass up to large highly complex forms, all possible body forms occur. Although the great majority are without symmetry, there are some which possess a definite symmetry. Thus bilateral symmetry is noted in all members of Diplomonadina (p. 272); radial symmetry in Gonium, Cyclonexis, etc.; and universal symmetry, in certain Heliozoa, Volvox, etc.

The fundamental component of the protozoan body is the protoplasm which is without exception differentiated into the nucleus and the cytosome. Haeckel's monera are now considered as nonexistent, since improved microscopic technique failed in recent years to reveal any anucleated protozoans. The nucleus and the cytosome are inseparably important to the well-being of a protozoan, as has been shown by numerous investigators since Verworn's pioneer work. In all cases, successful regeneration of the body is only accomplished by the nucleus-bearing portions and enucleate parts degenerate soon or later. On the other hand, when the nucleus is taken out of a cell, both the nucleus and cytosome degenerate, which indicate their intimate association in carrying on the activities of the body. It appears certain that the nucleus controls the assimilative phase of metab-

olism which takes place in the cytosome in normal animals, while the cytosome is capable of carrying on catabolic phase of the metabolism. Aside from the importance as the controlling center of metabolism, evidences point to the conclusion that the nucleus contains the genes or hereditary factors which characterize each species of protozoans from generation to generation, as in the cells of multicellular animals and plants.

The nucleus

Because of a great variety of external body forms and of consequent body organizations, the protozoan nuclei are of various forms, sizes and structures. At one extreme there is a small nucleus and, at the other, a large voluminous one and, between these extremes, is found every conceivable variety of form and structure. The majority of Protozoa contain a single nucleus, though many may possess two or more throughout the greater part of their life-cycle. In several species, each individual possesses two similar nuclei, as in *Pelomyxa binucleata*, *Arcella vulgaris*, Diplomonadina, Protoopalina and Zelleriella. In Euciliata and Suctoria, two dissimilar nuclei, a macronucleus and a micronucleus, are typically present. The macronucleus is always larger than the micronucleus, and controls the trophic activities of the organism, while the micronucleus is concerned with the reproductive activity. Certain Protozoa possess numerous nuclei of similar structure, as for example, in Mycetozoa, Actinosphaerium, Opalina, Cepedea, Myxosporidia, Microsporidia, etc. *Dileptus anser* contains many small macronuclei, a condition not observed in other euciliates.

The essential components of the protozoan nucleus are the nuclear membrane, chromatin, plastin and nucleoplasm. Their interrelationship varies sometimes from one developmental stage to another, and vastly among different species. Structurally, they fall in general into one of the two types: vesicular and compact.

The **vesicular** nucleus (Fig. 2, *a*) consists of a nuclear membrane which is sometimes very delicate, but distinct, nucleoplasm and chromatin. Besides there is an intranuclear body which is, as a rule, more or less spherical and which appears to be of different make-ups, as judged by its staining reactions among different nuclei. It may be composed of chromatin, of plastin, or of a mixture of both. The first type is sometimes called karyosome

and the second, nucleolus or plasmosome. Absolute distinction between these two terms cannot be made as they are based upon the difference in affinity to nuclear stains which cannot be standardized and hence do not give uniformly the same result. Following Minchin and others, the term endosome is advocated here to designate one or more conspicuous bodies other than the chromatin granules, present within the nuclear membrane.

When viewed in life, the nucleoplasm is ordinarily homogeneous and structureless. But, upon fixation, there appear invariably plastin strands or networks which seem to connect the

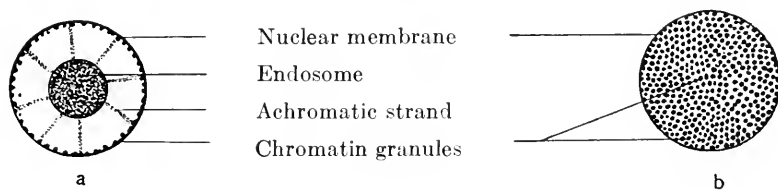


FIG. 2. a, vesicular nucleus; b, compact nucleus (diagrams).

endosome and the nuclear membrane. Some investigators hold that these strands or networks exist naturally in life, but due to the similarity of refractive indices of the strands and of the nucleoplasm, they are not visible and that, when fixed, they become readily recognizable because of a change in these indices. In some nuclei, however, certain strands have been observed in life, as for example in the nucleus of the species of *Barbulanympha* (Fig. 131, c), according to Cleveland and his associates (1934). Others maintain that the achromatic structures prominent in fixed vesicular nuclei are mere artifacts brought about by fixation and do not exist in life and that the nucleoplasm is a homogeneous liquid matrix of the nucleus.

The chromatin substance is ordinarily present as small granules although at times they may be in block forms. Precise knowledge of chromatin is still lacking. At present the determination of the chromatin depends upon the following tests: 1) artificial digestion which does not destroy this substance, while non-chromatinic parts of the nucleus are completely dissolved; 2) acidified methyl green which stains the chromatin bright green; 3) 10 per cent sodium chloride solution which dissolves, or causes swelling of, chromatin granules, while nuclear membrane and achromatic substances remain unattacked; and 4) in the fixed condition

Feulgen's nucleal reaction. The vesicular nucleus is most commonly present in various orders of the Sarcodina and Mastigophora.

The **compact** nucleus (Fig. 2, *b*), on the other hand, contains a large amount of chromatin substance and a comparatively small amount of nucleoplasm, and is thus massive. The macronucleus of the Ciliophora is almost always of this kind. The variety of forms of the compact nuclei is indeed remarkable. It may be spherical, ovate, cylindrical, club-shaped, band-form, moniliform, horseshoe-form, filamentous, or root-like. The nuclear membrane is always distinct, and the chromatin substance is usually spheroidal, varying in size among different species and often even in the same nucleus. In the majority of species, the chromatin granules are small and compact, though in some forms, such as *Nyctotherus ovalis* (Fig. 3), they may reach 20μ or more in diameter, and while the smaller chromatin granules seem to be solid, larger forms contain alveoli of different sizes in which smaller chromatin granules are suspended (Kudo, 1936).

There is no sharp demarcation between the vesicular and compact nuclei, since there are numerous nuclei the structures of which are intermediate between the two. Moreover what appears to be a vesicular nucleus in life, may approach a compact nucleus when fixed and stained as in the case of Euglenoidina. Several experimental observations show that the number, size, and structure of the endosomes in the vesicular nucleus, and the amount and arrangement of the chromatin in the compact nucleus, vary according to the physiological state of the protozoan concerned. The macronucleus may be divided into two or more parts with or without connections among them and in *Dileptus anser* into more than 200 small nuclei, each of which is "composed of a plastin core and a chromatin cortex" (Calkins; Hayes).

In general, the chromatin granules or spherules fill the intranuclear space compactly, in which one or more endosomes may occur. In many nuclei these chromatin granules appear to be suspended freely, while in others a reticulum appears to make the background. The chromatin of compact nuclei gives a strong positive Feulgen's nucleal reaction. The macronuclear and micronuclear chromatin substance responds differently to Feulgen's nucleal reaction or to the so-called nuclear stains, as judged by the difference in the intensity or tone of color. In *Paramecium*

caudatum, *P. aurelia*, *Chilodonella*, *Nyetotherus ovalis*, etc., the macronuclear chromatin is colored more deeply than the micronuclear chromatin, while in *Colpoda*, *Urostyla*, *Euplotes*, *Stylonychia*, and others, the reverse seems to be the case, which may support the validity of assumption that the two types of the

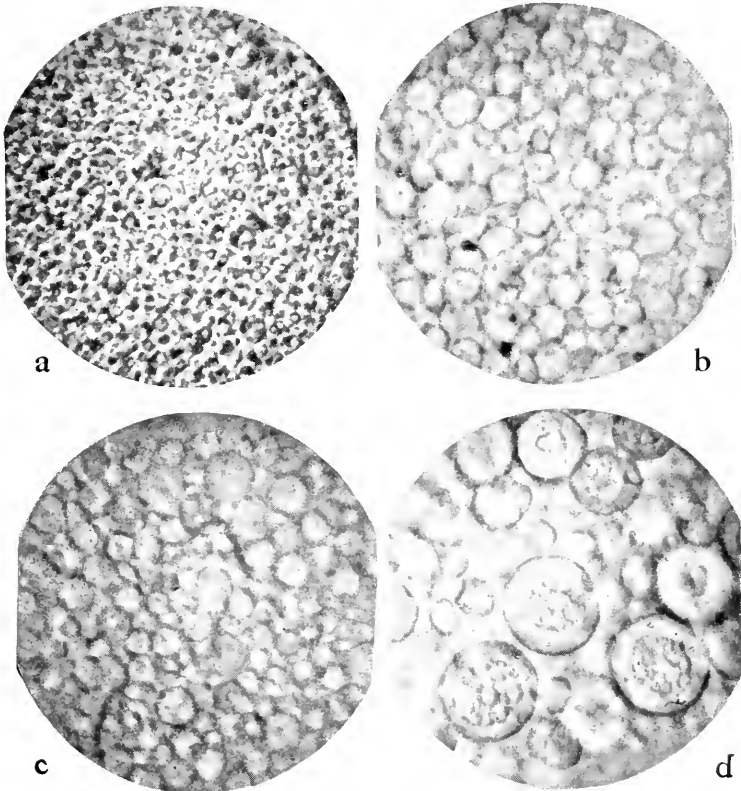


FIG. 3. Four macronuclei of *Nyetotherus ovalis*, showing chromatin spherules of different sizes, $\times 650$ (Kudo).

nuclei of *Euciliata* and *Suctorina* are made up of different chromatin substances—idiochromatin in the micronucleus and trophochromatin in the macronucleus—and in other classes of Protozoa, the two kinds of chromatin are present together in a single nucleus.

Chromidia. Since the detection of chromatin had solely depended on its affinity to nuclear stains, several investigators

found extranuclear chromatin granules in many protozoans. Finding such granules in the cytosome of *Actinosphaerium eichhorni*, *Arcella vulgaris*, and others, Hertwig (1902) called them chromidia, and maintained that under certain circumstances, such as lack of food material, the nuclei disappear and the chromatin granules become scattered throughout the cytosome. In the case of *Arcella vulgaris*, the two nuclei break down completely to produce a chromidial-net which later reforms into smaller secondary nuclei. It has, however, been found by Bělař that the lack of food caused the encystment rather than chromidia-formation in *Actinosphaerium* and, according to Reichenow, Jollos observed that in *Arcella* the nuclei persisted, but were thickly covered by chromidial-net which could be cleared away by artificial digestion to reveal the two nuclei. In *Diffugia*, the chromidial-net is vacuolated or alveolated in the fall and in each alveolus appear glycogen granules which seem to serve as reserve food material for the reproduction that takes place during that season (Zuelzer), and the chromidia occurring in *Actinosphaerium* appear to be of a combination of a carbohydrate and a protein (Rumjantzew and Wermel). Apparently the widely distributed volutin (p. 95), and many inclusions or cytozoic parasites, such as *Sphaerita*, which occur occasionally in different *Sarcodina*, have in some cases been called chromidia. By using Feulgen's nuclear reaction, Reichenow (1928) obtained a diffused violet-stained zone in *Chlamydomonas* and held them to be dissolved volutin. Calkins (1933) found the chromidia of *Arcella vulgaris* negative to the nuclear reaction, but by omitting acid-hydrolysis and treating with fuchsin-sulphurous acid for 8-14 hours, the chromidia and the secondary nuclei were found to show a typical positive reaction and believed that the chromidia are chromatin. Thus at present the real nature of chromidia is still not clearly known, although many protozoologists are inclined to think that the substance is not chromatinic, but, in some way, is connected with the metabolism of the protozoan.

The cytosome

The extranuclear part of the protozoan body is the cytosome. It is composed of the cytoplasm, a colloidal system, which may be homogenous, granulated, vacuolated, reticulated, or fibrillar in optical texture, and is almost always colorless. The chromato-

phore-bearing Protozoa are variously colored, and those with symbiotic algae or cryptomonads are also greenish or brownish in color. Furthermore, pigment or crystals which are produced in the body, may give protozoans various colorations. In several forms pigments are diffused throughout the cytoplasm. For example, many dinoflagellates are beautifully colored which, according to Kofoed and Swezy, is due to a thorough diffusion of pigment in the cytoplasm. *Stentor coeruleus* is ordinarily blue-colored, the pigment responsible for which was called *Stentorin* (Lankester) and is lodged in granules between the surface striae; and rose- or purple-coloration of several species of *Blepharisma* appears to be due to a special pigment, *zoopurpurin* (Arcichovskij) which is lodged in the ectoplasmic granules often called protrichocysts (p. 65). The development of zoopurpurin is definitely correlated with the sun-light, as shown by Giese. Deeply pink specimens will lose color completely in a few hours when exposed to strong sun-light and the recoloration takes place in darkness very slowly.

The extent and nature of the cytosomic differentiation differs greatly among various groups. In the majority of Protozoa, the cytoplasm is differentiated into the ectoplasm and the endoplasm. The **ectoplasm** is the cortical zone which is hyaline and homogeneous. In the Ciliophora, it is a permanent and distinct part of the body and contains several organellae; in the Sarcodina and the Sporozoa, it is more or less a temporarily differentiated zone and hence varies greatly at different times and, in the Mastigophora, it seems to be more or less permanent. The **endoplasm** is more voluminous and fluid. It is granulated or alveolated and contains various organellae. While the alveolated cytoplasm is normal in forms such as the members of Heliozoa and Radiolaria, in other cases the alveolation of normally granulated or vacuolated cytoplasm indicates invariably the degeneration of the protozoan body.

In numerous Sarcodina and certain Mastigophora, the body surface is naked and not protected by any form-giving organella. According to observations by Kite, Howland, and others, the surface layer is not only elastic, but solid, and therefore the name **plasma-membrane** may be applied to it. Such forms are capable of undergoing amoeboid movement by formation of pseudopodia and by continuous change of form due to the movement of the

cytoplasm which is more fluid. However, the majority of Protozoa possess a characteristic and constant body form due to the development of a special envelope, the **pellicle**. In *Amoeba striata* and *A. verrucosa*, there is an extremely thin pellicle. The same is true with some flagellates, such as certain species of *Euglena*, *Peranema*, and *Astasia*, in which it is elastic and expansible so that the organisms possess a great deal of plasticity.

The pellicle of a ciliate is much thicker and more definite, and often variously ridged or sculptured. In many, linear furrows and ridges run longitudinally, obliquely, or spirally; and, in others, the ridges are combined with hexagonal or rectangular depressed areas. Still in others, such as *Coleps*, elevated platelets are arranged parallel to the longitudinal axis of the body as four girdles. In certain peritrichous ciliates, such as *Vorticella monilata*, *Carchesium granulatum*, etc., the pellicle may possess nodular thickenings arranged in more or less parallel rows at right angles to the body axis.

While the pellicle always covers the protozoan body closely, there are other kinds of protective envelopes produced by Protozoa which may cover the body rather loosely. These are the shell, test, lorica or envelope. The **shell** of various Phytomastigina is mainly made up of cellulose, a carbohydrate, which is widely distributed among the plant kingdom. It may be composed of a single or several layers, and may possess ridges or markings of various patterns on it. In addition to the shell, gelatinous substance may in many forms be produced to surround the shelled body or in the members of Volvocidae to form the matrix of the entire colony in which the individuals are imbedded. In the dinoflagellates, the shell is highly developed, and often composed of numerous plates which are variously sculptured.

In other Protozoa, the shell is made up of chitin or pseudo-chitin (tectin). Common examples are found in the testaceans; for example, in *Arcella* and allied forms, the shell is made up of chitinous material, constructed in particular ways which characterize the different genera. Newly formed shell is colorless, but older ones become brownish, because of the presence of iron oxide. Diffugia and related genera form shells by glueing together small sand-grains, diatom-shells, debris, etc., with chitinous or pseudo-chitinous substances which they secrete. Many foraminiferans seem to possess a remarkable selective power in the use of foreign

material for the construction of their shells. According to Cushman, *Psammospaera fusca* uses sand-grains of uniform color but of different sizes, while *P. parva* uses grains of more or less uniform size but adds, as a rule, a single large acerose sponge spicule which is built into the test and which extends out both ways considerably. Cushman thinks that this is not accidental, since the specimens without the spicules are few and those with a short or broken spicules are not found. *P. bowmanni*, on the other hand, uses only mica flakes which are found in a comparatively small amount, and *P. rustica* uses acerose sponge spicules for the

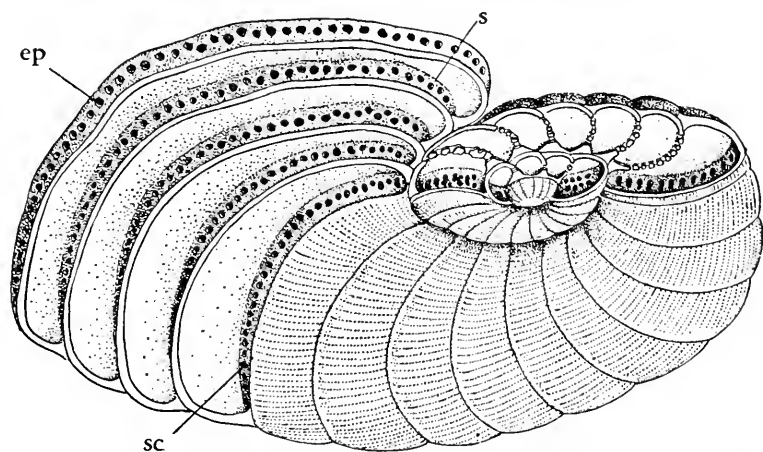


FIG. 4. Diagram of the shell of *Peneroplis pertusus*, \times about 35 (Carpenter). ep, external pore; s, septum; sc, stolon canal.

framework of the shell, skillfully fitting smaller broken pieces into polygonal areas. Other foraminiferans combine chitinous secretion with calcium carbonate and produce beautifully complicated shells (Fig. 4) with one or numerous pores. In the Coccolithidae, variously shaped platelets of calcium carbonate ornament the shell.

The silica is present further in the shells of various Protozoa. In Euglypha and related testaceans, siliceous scales or platelets are produced in the endoplasm and compose a new shell at the time of fission or of encystment together with the chitinous secretion. In many heliozoans, siliceous substance forms spicules, platelets, or combination of both which are embedded in the mucilaginous envelope which surrounds the body and, in some

cases, a special clathrate shell composed of silica, is to be found. In some Radiolaria, isolated siliceous spicules occur as in Heliozoa, while in others the lateral development of the spines results in production of highly complex and most beautiful shells with various ornamentations or incorporation of foreign material. Many pelagic radiolarians possess numerous conspicuous radiating spines in connection with the skeleton, which apparently aid the organisms to maintain their existence in the open sea.

Some flagellates may be encased in a chitinous **lorica** or house and in addition there is occasionally a **collar** developed at one end. The lorica found in the Ciliophora is mostly composed of chitinous substance alone, especially in Peritricha, although some produce a house made up of gelatinous secretion containing foreign material as in Stentor (p. 581). In the Tintinnidiidae, the loricae are either solely chitinous in numerous marine forms not mentioned in the present work or composed of sand-grains or coccoliths cemented together by chitinous secretion.

Locomotor organellae

Closely associated with the body surface are the organellae of locomotion: *pseudopodia*, *flagella*, and *cilia*. These organellae are not confined to Protozoa alone and occur in various cells of Metazoa. All protoplasmic masses are capable of movement which may result in change of their forms.

Pseudopodia. A pseudopodium is a temporary projection of part of the cytoplasm of those protozoans which do not possess a definite pellicle. Pseudopodia are therefore a characteristic organella of Sarcodina, though many Mastigophora and certain Sporozoa, which lack a pellicle, are able also to produce them. According to their form and structure, four kinds of pseudopodia are distinguished.

1). The **lobopodium** is formed by an extension of the ectoplasm and by a flow of endoplasm as is commonly found in *Amoeba proteus* (Figs. 42; 140). It is finger- or tongue-like, sometimes branched, and its distal end is typically rounded. It is quickly formed and equally quickly retracted. In many cases, there are many pseudopodia formed from the entire body surface, in which the largest one will counteract the smaller ones and the organism will move in one direction; while in others, there may be a single pseudopodium formed, as in *Amoeba striata*, *A. guttula*,

Vahlkampfia limax, *Pyxidicula operculata*, etc., in which case it is a broadly tongue-like extension of the body in one direction and the progressive movement of the organisms is comparatively rapid. The lobopodia may occasionally be conical in general shape, as in *Amoeba spumosa*. Although ordinarily the formation of lobopodia is by general flow of the cytoplasm, in some it is sudden and "eruptive," as in *Endamoeba blattae* or *Entamoeba histolytica* in which the flow of the endoplasm presses against the inner zone of the ectoplasm and the accumulated pressure finally causes breaks through the line, resulting in a sudden extension of the endoplasmic flow at that point.

2). The **filopodium** is a more or less filamentous projection composed almost exclusively of the ectoplasm. It may sometimes be branched, but the branches do not anastomose. Many testaceans, such as *Lecythium*, *Boderia*, *Plagiophrys*, *Pamphagus*, *Euglypha*, etc., form this type of pseudopodia. The pseudopodia of *Amoeba radiosa* may be considered as approaching this type more than the lobopodia.

3). The **rhizopodium** is also filamentous, but branching and anastomosing. It is found in numerous Foraminifera, such as *Elphidium*, *Peneroplis* (Fig. 5), etc., and in certain testaceans, such as *Lieberkuhnia*, *Myxotheca*, etc. The abundantly branching and anastomosing rhizopodia often produce a large network which serve almost exclusively for capturing prey.

4). The **axopodium** is, unlike the other three types, a more or less semi-permanent structure and composed of axial rod and cytoplasmic envelope. The axopodia are found in many Heliozoa, such as *Actinophrys*, *Actinosphaerium*, *Camptonema*, *Sphaerastrium*, and *Acanthocystis*. The axial rod, which is composed of fibrils (Doflein; Roskin), arises from the central body or the nucleus located in the approximate center of the body, from each of the nuclei in multinucleate forms, or from the zone between the ectoplasm and endoplasm (Fig. 6). Although semipermanent in structure, the axial rod is easily absorbed and reformed. In the genera of Heliozoa, not mentioned above and in numerous radiolarians, the radiating filamentous pseudopodia are so extremely delicate that it is difficult to determine whether an axial rod exists in each or not, although they resemble axopodia in general appearance.

There is no sharp demarcation between the four types of

pseudopodia, as there are transitional pseudopodia between any two of them. For example, the pseudopodia formed by *Arcella*, *Lesquereusia*, *Hyalosphaenia*, etc., resemble more lobopodia

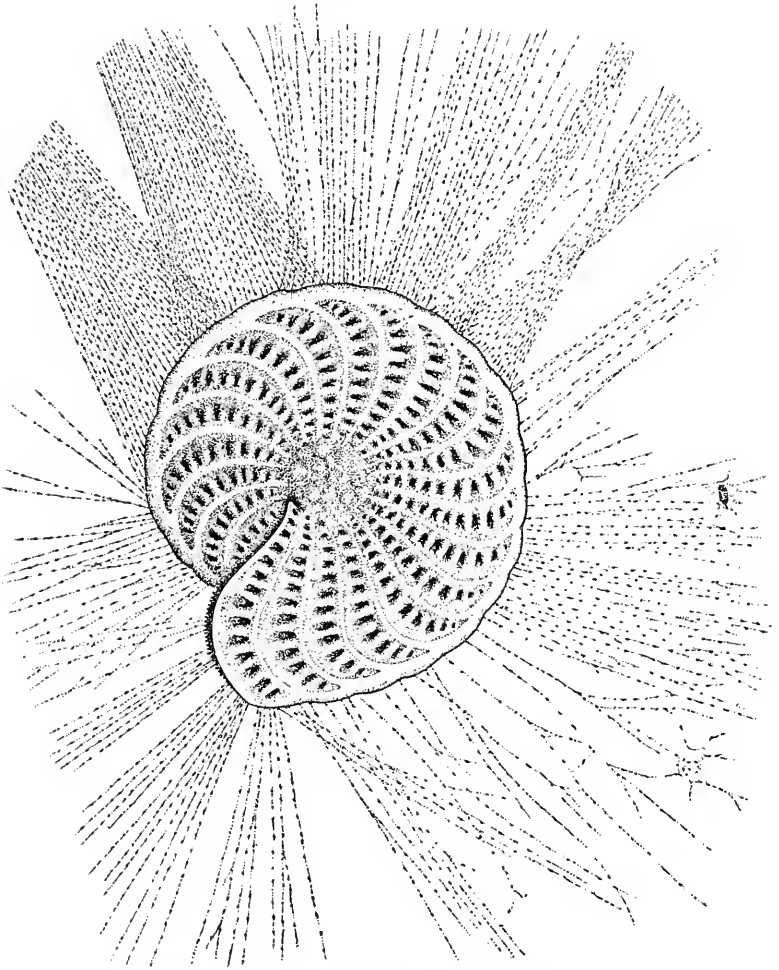


FIG. 5. Pseudopodia of *Elphidium strigilata*, \times about 50
(Schulze from Kühn).

than filopodia, though composed of the ectoplasm only. The pseudopodia of *Actinomonas*, *Elacorhanis*, *Clathrulina*, etc., may be looked upon as transitional between rhizopodia and axopodia.

While the pseudopodia formed by an individual are usually of characteristic form and appearance, they may show an entirely different appearance under different circumstances. According to the often-quoted experiment of Verworn, limax amoebae change into *radiosa* amoebae upon addition of potassium hydrate to the water (Fig. 7). Mast has recently shown that when *Amoeba proteus* or *A. dubia* is transferred into pure water, the amoeba produced radiating pseudopodia, and when transferred to a salt

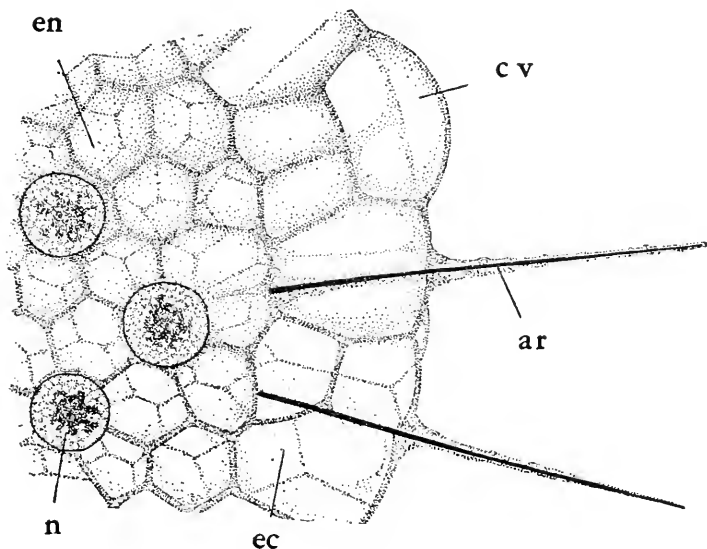


FIG. 6. Portion of *Actinosphaerium eichhorni*, $\times 800$ (Kühn). ar, axial rod; cv, contractile vacuole; ec, ectoplasm; en, endoplasm; n, nucleus.

medium, it changed into monopodial form, which change, he was inclined to attribute to the difference in the water contents of the amoeba. In some cases during and after certain internal changes, an amoeba may show conspicuous differences in pseudopodia (Neresheimer). As was stated before, pseudopodia occur widely in forms which are placed under classes other than Sarcodina during a part of their life-cycle. Care, therefore, should be exercised in using them for taxonomic consideration of the Protozoa.

Flagella. The flagellum is a filamentous extension of the cytoplasm and is ordinarily extremely fine and highly vibratile, so

that it is difficult to recognize it in life under the microscope with a moderate magnification. In a number of species, the flagellum, however, can be seen in life as a long filament, as for example in *Peranema*. As a rule, the number of flagella present in a single individual is small, varying from one to eight, but in *Hypermastigia* there are numerous flagella. A flagellum appears to be composed of at least two parts (Fig. 8, *a*, *b*). An axial filament which is elastic, takes its origin directly, or indirectly through

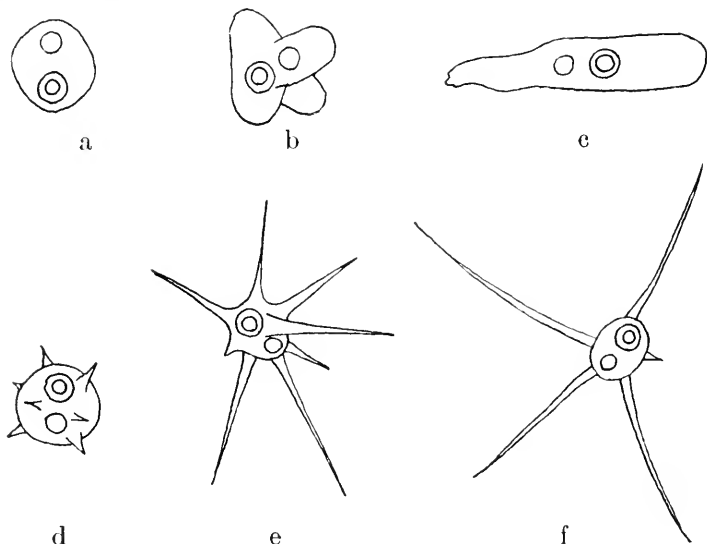


FIG. 7. Form-change in a limax-amoeba (Verworn). *a*, *b*, contracted forms; *c*, individual showing typical form; *d*-*f*, radiosa-forms, after addition of KOH solution to the water.

basal granule, in the blepharoplast. Surrounding this filament there is a sheath of contractile cytoplasm which varies in thickness alternately on the opposite sides of the filament. The flagellum ordinarily tapers toward its distal end where the axial filament is said to be frequently exposed.

Recently Vlk found, besides the kind above mentioned which he called the whip-flagellum, another form named by him as the ciliary flagellum. The latter is said to be uniformly thick, but possesses dense ciliary projections which are arranged on a flagellum in one or two spiral rows (Fig. 8, *c*, *d*). Vlk found the whip-flagellum in *Chlamydomonas*, *Polytoma uvella*(*e*), *Cercomonas*

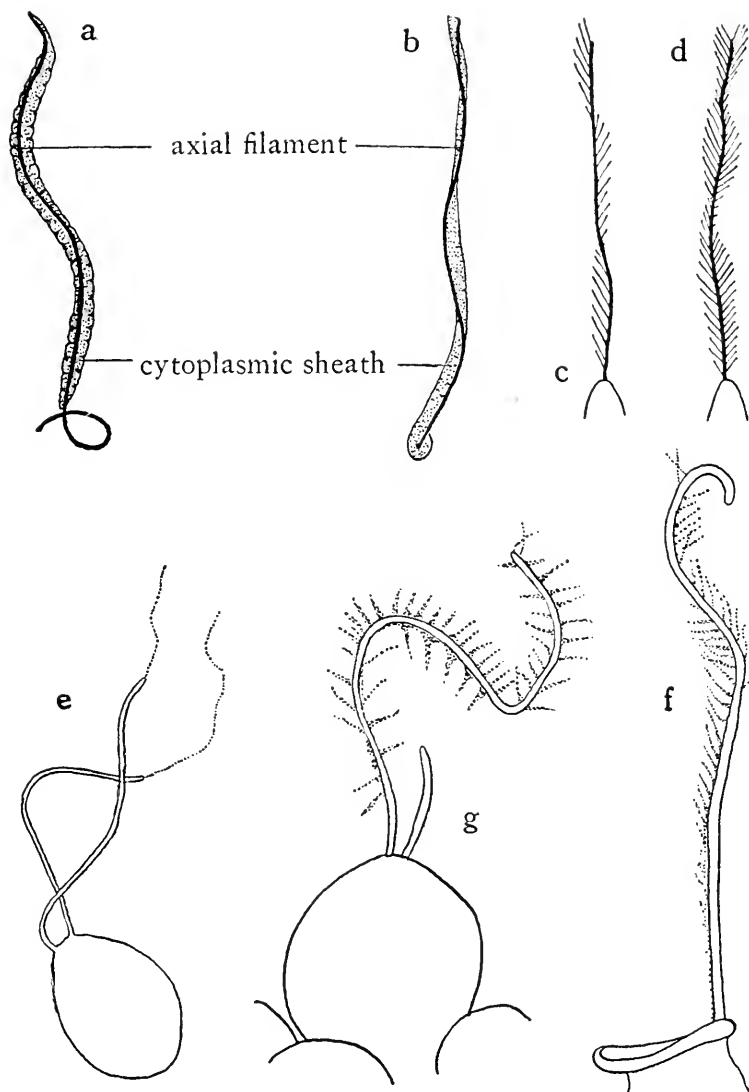


FIG. 8. Diagrams of flagella. a, flagellum of *Euglena* (Bütschli); b, flagellum of *Trachelomonas* (Plenge); c, ciliary flagellum with one row of cilia; d, a ciliary flagellum with two rows of cilia; e, whip-flagella of *Polytoma uvella*; f, ciliary flagellum of *Urceolus cyclostomus*; g, the flagella of *Monas socialis* (Vlk).

crassicauda, *Trepomonas rotans*, *T. agilis*, *Heramita inflata*, *Urophagus rostratus*, etc.; the ciliary flagellum, in *Mallomonas*, *Chromulina*, *Trachelomonas*, *Urceolus* (*f*), *Phacus*, *Euglena*, *Astasia*, *Distigma*, etc.; and both kinds in *Synura*, *Uroglena*, *Dinobryon*, *Monas* (*g*), etc.

The flagellum is most frequently inserted near the anterior end of the body and directed forward, its movement pulling the organism forward. Combined with this, there may be a trailing flagellum which is directed posteriorly and which serves to steer

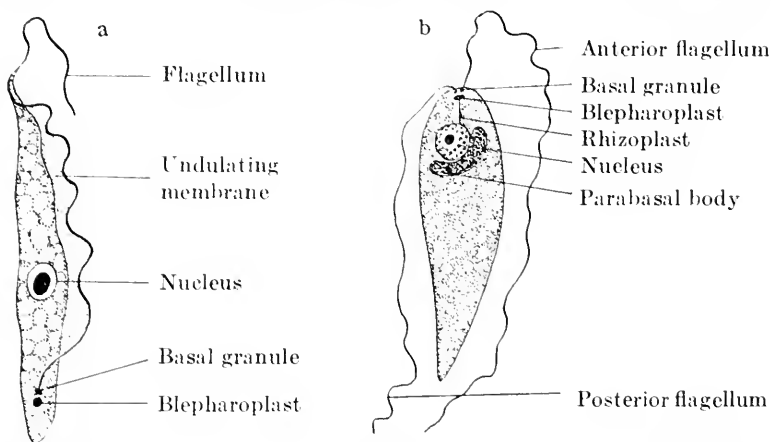


FIG. 9. Diagrams of two flagellates, showing their structures (Kühn).
a, *Trypanosoma brucei*; b, *Proteromonas lacertae*.

the course of movement or to push the body forward to a certain extent. In a comparatively small number of flagellates, the flagellum is inserted near the posterior end of the body and would push the body forward by its vibration. Lankester coined *tractella* and *pulsella* for pulling and pushing flagella respectively.

In certain parasitic *Mastigophora*, such as *Trypanosoma* (Fig. 9, a), *Trichomonas*, etc., there is a very delicate membrane extending out from the side of the body, a flagellum bordering its outer margin. When this membrane vibrates, it shows a characteristic undulating movement, as will easily be seen in *Trypanosoma rotatorium* of the frog, and is called the **undulating membrane**. In many of the dinoflagellates, the transverse flagellum seems to be similarly constructed (Kofoid and Swezy) (Fig. 101, d, f).

Cilia. The cilia are the organella of locomotion and food-capturing found in the Ciliophora. They seem to serve often as a tactile organella. The cilia are fine and more or less short processes of ectoplasm and occur in large numbers in the majority of the Holotricha. They may be uniformly long, as in Protociliata, or may be of different lengths, being longer at the extremities, on certain surfaces, in peristome or in circumoral areas. Ordinarily the cilia are arranged in longitudinal, oblique, or spiral rows, being inserted on either the ridges or the furrows. Again the cilia may be confined to certain parts or zones of the body.

Each cilium originates in a basal granule situated in the deeper part of the ectoplasm and, in a few species, a cilium is found to be made up of an elastic axial filament arising from the basal granule and contractile sheath. Gelei observed in flagella and cilia, lipoid substance in granular or rod-like forms which differed even among different individuals of the same species; and Klein found in many cilia of *Colpidium colpoda*, an argentophilous substance in granular form much resembling the lipoid structure of Gelei and called them "cross-striation" of the contractile component (Fig. 10).

The cilia are often present in a certain area more densely than in other parts of body and, consequently, such an area stands out conspicuously, and is sometimes referred to as a ciliary field. If this area is in the form of a zone, it may be called a ciliary zone. Some authors use pectinellae for short longitudinal rows or transverse bands of close-set cilia. In a number of forms, such as *Coleps Stentor*, etc., there occur, mingled among the vibratile cilia, immobile stiff cilia which are apparently solely tactile in function.

In the Hypotricha, the cilia are largely replaced by cirri, although in some species both may occur. A **cirrus** is composed of a number of cilia arranged in 2 to 3 rows which fused into one structure completely (Figs. 11, 12), which was demonstrated by Taylor. Klein also showed by desiccation that each marginal cirrus of *Stylonychia* was composed of 7 to 8 cilia. In some instances, the distal portion of a cirrus may show two or more branches. The cirri are confined to the ventral surface in Hypotricha, and called frontal, ventral, anal, caudal, and marginal cirri, according to their location (Fig. 11). Unlike the cilia, the cirri may beat in any direction so that the organisms bearing them, show various ways of locomotion. *Oxytricha*, *Stylonychia*,

etc., walk on frontals, ventrals, and anals, while swimming movement by other species is of different types.

In all euciliates except Holotricha, there are adoral membranelae. A **membranella** is composed of a double ciliary lamella, fused completely into a plate (Fig. 12). A number of these membranelae occur on a margin of the peristome, forming the **adoral zone**

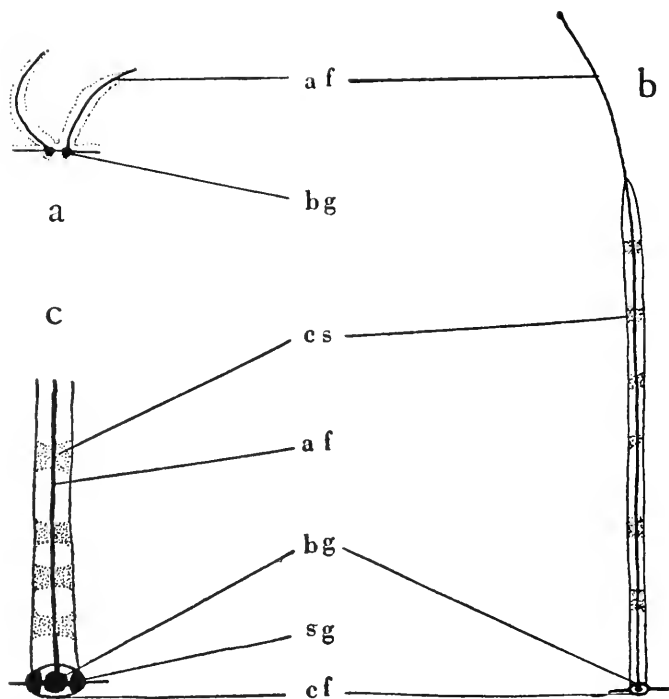
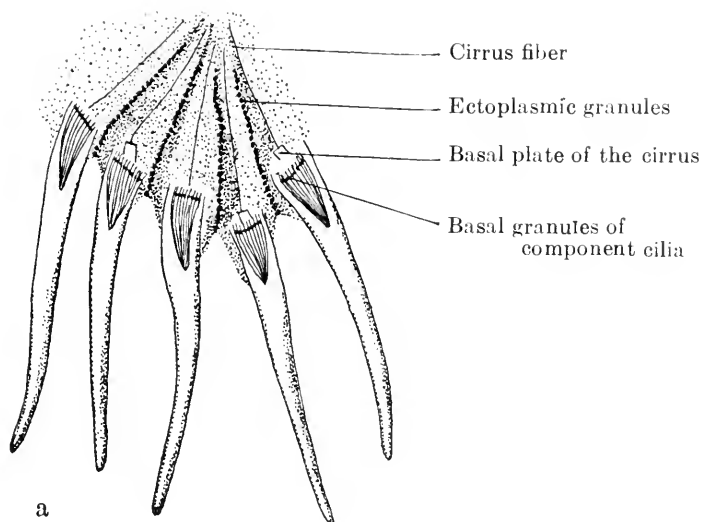
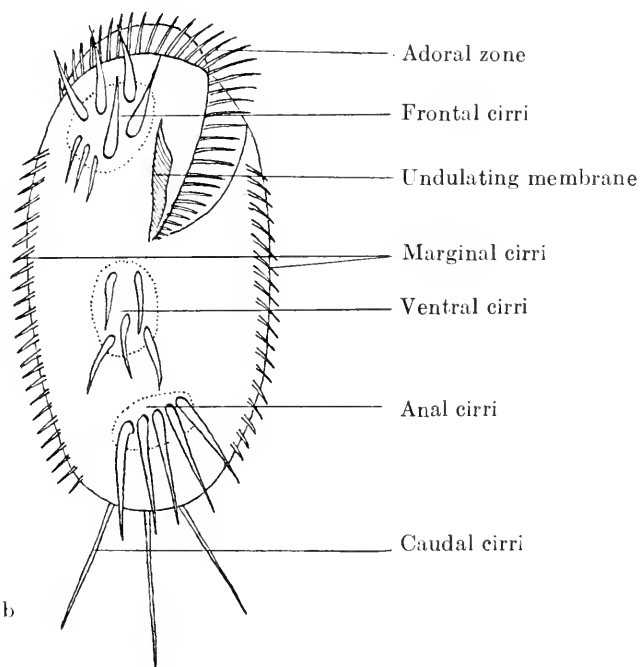


FIG. 10. Diagrams of cilia (Klein). a, *Coleps*; b, *Cyclidium glaucoma*; c, *Colpidium colpoda*. af, axial filament; bg, basal granule; cf, circular fibril; cs, cross-striation; sg, secondary granule.

of membranelae, which serves for bringing the food particles to the cytostome. The frontal portion of the zone, the so-called **frontal membrane**, appears to serve for locomotion and Kahl considers that it is probably made up of three lamellae. The membranes which are often found in Holotricha and Heterotricha, are transparent thin membranous structures composed of one or two rows of cilia, which are more or less strongly fused.



a



b

FIG. 11. a, five anal cirri of *Euplotes patella* (Taylor); b, schematic ventral view of *Stylonychia* to show the distribution of the cirri.

The membranes, located in the lower end of the peristome, are sometimes called perioral membranes, and those in the cytopharynx, undulating membranes.

In Suctoria, cilia are present only during the developmental stages, and, as the organisms become mature, tentacles are developed. The **tentacles** are concerned with food-capturing, and are either prehensile or usually suctorial. In a few instances the

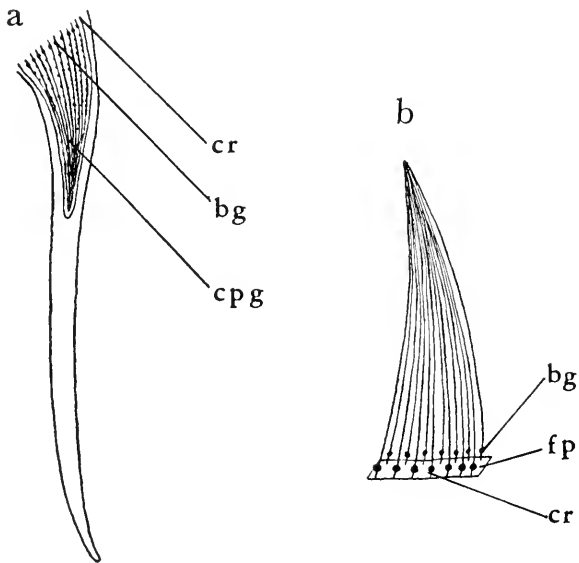


FIG. 12. Diagrams of cirrus and membranella of *Euplotes patella*, $\times 1450$ (Taylor). a, an anal cirrus in side view; b, a membranella; bg, basal granule; cpg, coagulated protoplasmic granules; cr, ciliary root; fp, fiber plate.

tentacles are tubular and this type is interpreted by Collin as possibly derived from a cytostome and cytopharynx of the ciliate (Fig. 13).

Although the vast majority of Protozoa possess only one of the three organellae of locomotion mentioned above, a few may possess pseudopodia in one phase and flagella in another phase during their life-cycle. Among many examples, may be mentioned *Dimastigamoebidae* (Fig. 139), *Tetramitus rostratus* (Fig. 122), etc. Furthermore, there are some protozoans which possess two types of organellae at the same time. Flagellum or flagella

and pseudopodia occur in many Phytomastigina and Rhizomastigina, and a flagellum and cilia are present in *Ileonema* (Fig. 235, b, c).

In the cytosome of Protozoa there occur various organelles, each of which will be considered briefly here.

Fibrillar structures

One of the characteristics of the protoplasm is its contractility. If a fully expanded *Amoeba proteus* is subjected to a mechanical pressure, it retracts its pseudopodia and contracts into a more or less spherical form. In this response there is no special organella, and the whole body reacts. But in certain other Protozoa, there

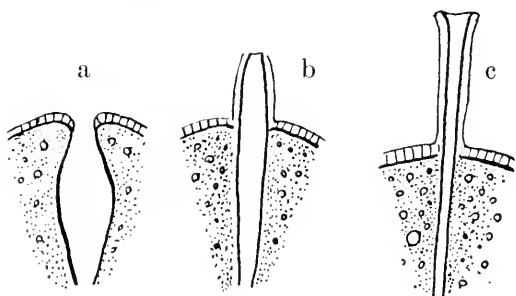


FIG. 13. Diagrams showing the possible development of a suckorial tentacle from a cytostome and cytopharynx of a ciliate (Collin).

are special organelles of contraction. Many Ciliophora are able to contract instantaneously when subjected to mechanical pressure, as will easily be noticed by following the movement of *Stentor*, *Spirostomum*, *Trachelocerca*, *Vorticella*, etc., under a dissecting microscope. The earliest observer of the contractile elements of Protozoa was Lieberkühn (1857) who noted "muscle fibers" in the ectoplasm of *Stentor* which were later named myonemes (Haeckel) or Neurophanes (Neresheimer).

The **myonemes** of *Stentor* have been studied by several investigators. According to Schröder (1906), there is a canal between each two longitudinal striae and in it occurs a long banded myoneme which measures in cross-section $3-7\mu$ high by about 1μ wide and which appears cross-striated (Fig. 14). Roskin (1923) considers that the myoneme is a homogeneous cytoplasm (kino-plasm) and the wall of the canal is highly elastic and counteracts

the contraction of the myonemes. All observers agree that the myoneme is a highly contractile organella.

Many stalked peritrichous ciliates have well-developed myonemes not only in the body proper, but also in the stalk. Koltzoff's studies show that the stalk is a pseudochitinous tube, enclosing an inner tube filled with granulated thecoplast, surrounding a

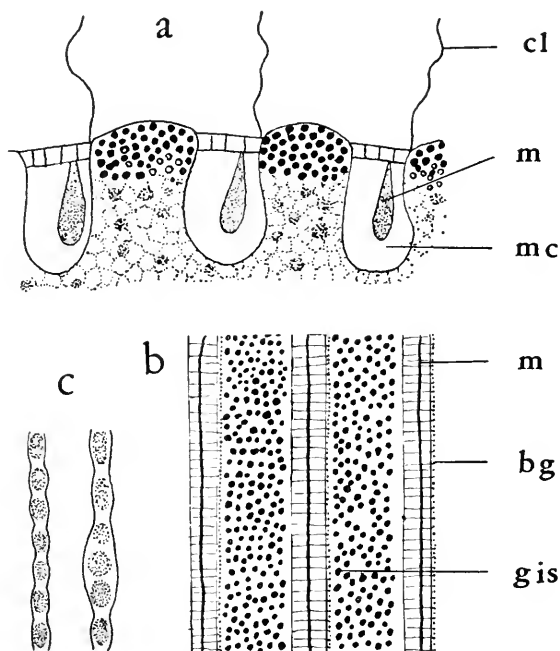


FIG. 14. Myonemes in *Stentor coeruleus* (Schröder). a, cross-section of ectoplasm; b, surface view of three myonemes; c, two isolated myonemes; bg, basal granules; cl, cilium; gis, granules between striae; m, myonemes; mc, myoneme canal.

central rod, composed of kinoplasm, on the surface of which are arranged skeletal fibrils (Fig. 15). The contraction of the stalk is brought about by the action of kinoplasm and walls, while elastic rods will lead to extension of the stalk. Myonemes present in the ciliates aid in the contraction of body, but those which occur in many Gregarinida aid apparently in locomotion, being arranged longitudinally, transversely and probably spirally (Fig. 15). In certain Radiolaria, such as *Acanthometron elasticum*

(Fig. 168, c), etc., each axial spine is connected with 10–30 myonemes (myophrisks) originating in the body surface. When these myonemes contract, the body volume is increased, thus in this case functioning as a hydrostatic organella.

In *Isotricha prostoma* and *I. intestinalis*, Schuberg (1888) observed that the nucleus is suspended by ectoplasmic fibrils and

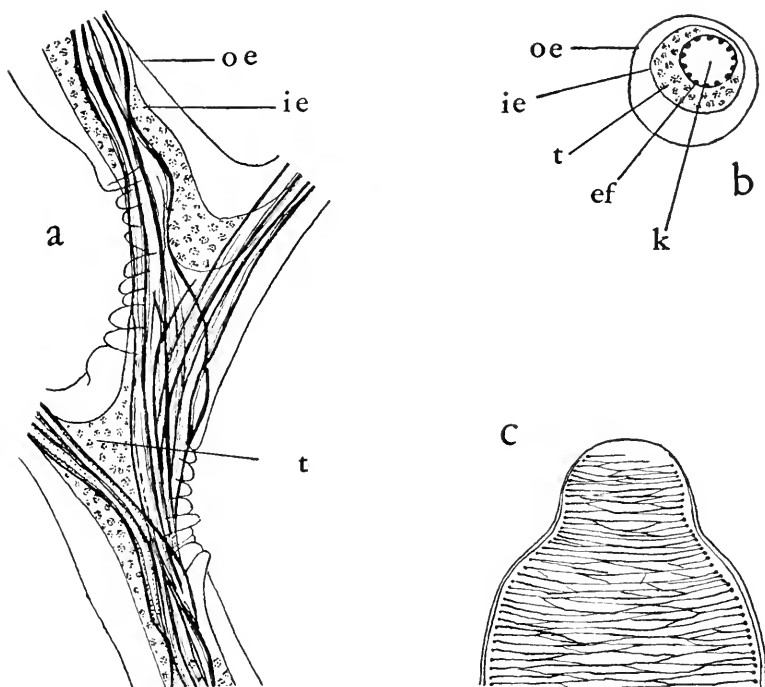


FIG. 15. a, b, fibrillar structures of the stalk of *Zoothamnium* (Koltzoff); c, myonemes in *Gregarina* (Schneider). ef, elastic fiber; ie, inner envelope; k, kinoplasm; oe, outer envelope; t, thecoplasm.

called the apparatus **karyophores**. In some forms these fibrils are replaced by ectoplasmic membranes as in *Nyctotherus ovalis* (Zuluta; Kudo). ten Kate (1927) studied fibrillar systems in *Opalina*, *Nyctotherus*, *Ichthyophthirius*, *Didinium*, and *Balantidium*, and found that there are numerous fibrils, each of which originates in a basal granule of a cilium and takes a transverse or oblique course through the endoplasm, ending in a basal granule located on the other side of body. He further noted that the cyto-

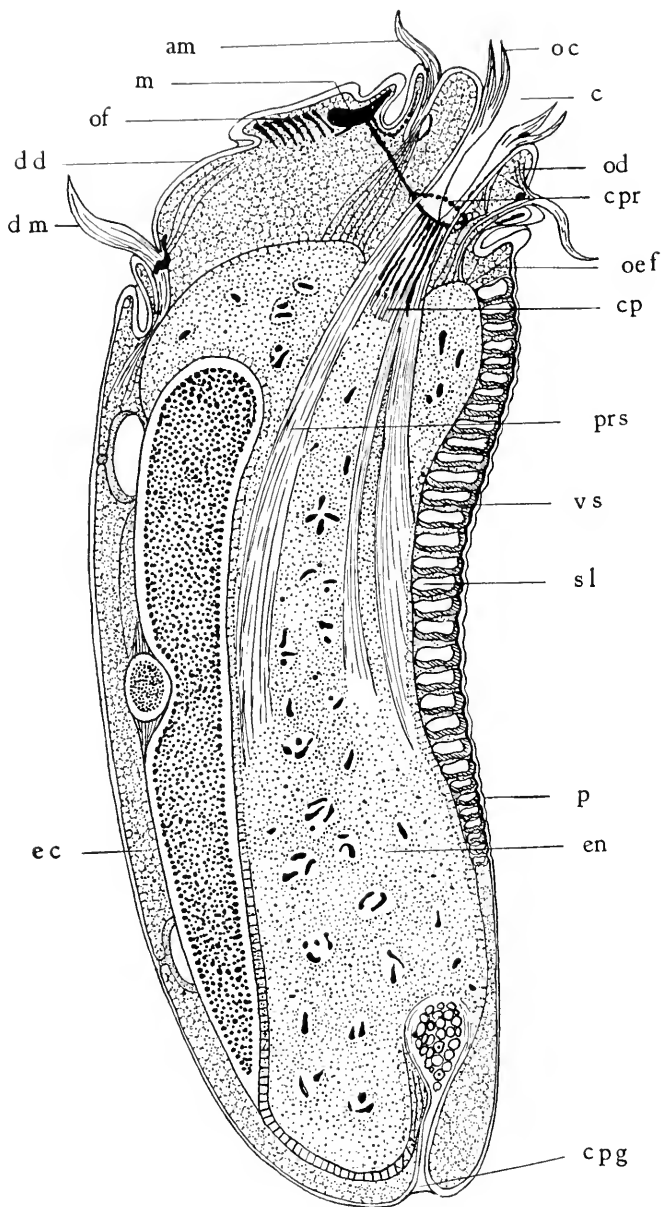


FIG. 16. A composite drawing from three median sagittal sections of *Epidinium ecaudatum*, fixed in Zenker and stained with Mallory's connective tissue stain, $\times 1200$ (Sharp). am, adoral membranellae; c, cytostome; cp, cytopharynx; cpg, cytopygus; cpr, circumpharyngeal ring; dd, dorsal disk; dm, dorsal membrane; ec, ectoplasm; en, endoplasm; m, motorium; oc, oral cilia; od, oral disk; oef, oesophageal fibers; of, opercular fibers; p, pellicle; prs, pharyngeal retractor strands; sl, skeletal laminae; vs, ventral skeletal area.

pharynx and nucleus are also connected with these fibrils. ten Kate suggested **morphonemes** for them, since he believed that the majority were form-retaining fibrils.

The well-coordinated movement of cilia in the ciliate has long been recognized, but it was Sharp (1914) who definitely showed that this ciliary coordination is made possible by a certain fibrillar system which he discovered in *Epidinium* (*Diplodinium*) *ecaudatum* (Fig. 16). Sharp recognized in this ciliate a complicated fibrillar system, connecting all the motor organellae of the cytostomal region, and thinking that it was "probably nervous in function," as its size, arrangement and location did not suggest supporting or contractile function, he gave the name **neuromotor apparatus** to the whole system. This apparatus consists of a central motor mass, the *motorium* (which is stained red with Zenker fixation and modified Mallory's connective tissue staining), located very deeply in the ectoplasm just above the base of the left skeletal area, from which definite strands radiate: namely, one to the roots of the dorsal membranellae (a dorsal motor strand); one to the roots of the adoral membranellae (a ventral motor strand); one to the cytopharynx (a circum-oesophageal ring and oesophageal fibers); and several strands into the ectoplasm of the operculum (opercular fibers). A similar apparatus has since been observed in many other ciliates: *Euplotes* (Yocom; Taylor), *Balantidium* (McDonald), *Paramecium* (Rees; Brown; Lund), *Tintinnopsis* (Cambell), *Boveria* (Pickard), *Dileptus* (Visscher), *Chlamydodon* (MacDougall), *Entorhipidium* and *Lechriopyla* (Lynch), *Eupoterion* (MacLennan and Connell), *Metopus* (Lucas), *Troglodytella* (Robertson), *Oxytricha* (Lund), *Ancistruma* and *Conchophthirus* (Kidder), etc.

Euplotes patella, a common free-living hypotrichous ciliate, has been known for nearly 50 years to possess definite fibrils connecting the anal cirri with the anterior part of the body. Engelmann suggested that their function was somewhat nerve-like, while others maintained that they were supporting or contracting in function. Yocom (1918) traced the fibrils to the motorium, a very small bilobed body (about 8μ by 2μ) located close to the right anterior corner of the triangular cytostome (Fig. 17). Joining with its left end are five long fibers from the anal cirri which converge and appear to unite with the motorium as a single strand. From the right end of the motorium extends the mem-

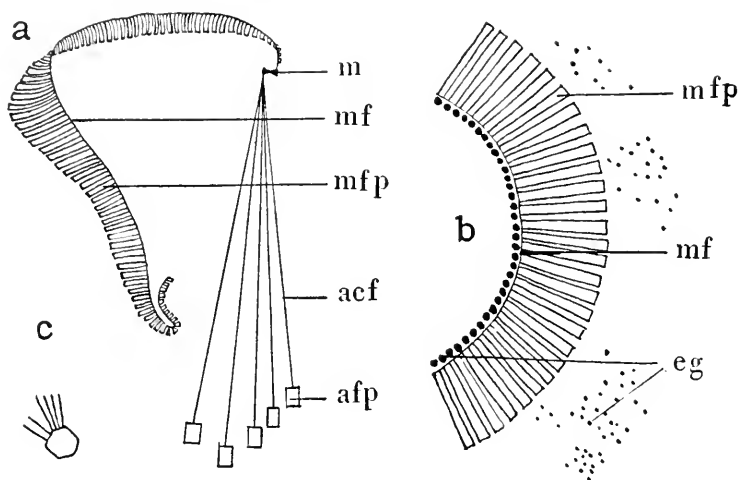


FIG. 17. Diagrams showing the neuromotor apparatus of *Euplotes patella* (Taylor). a, diagrammatic dorsal view of the entire apparatus, $\times 1600$; b, dissected portion of disintegrating membranella fiber plates attached to the membranella fiber; c, a dissociated fiber plate of a frontal cirrus with its attached fibers, $\times 1450$. acf, anal cirrus fiber; afp, anal fiber plate; eg, small and large ectoplasmic granules; m, motorium; mf, membranella fiber; mfp, membranella fiber plate.

branella-fiber anteriorly, and then to left along the proximal border of the oral lip and the bases of all membranellae. Yocom further noticed that within the lip there was a latticework structure whose bases very closely approximate the cytostomal fiber. Taylor (1920) recognized two additional groups of fibrils in the same organism: 1) membranella fiber plates, each of which is contiguous with a membranella basal plate, and is attached at one end to the membranella fiber; 2) dissociated fiber plates contiguous with the basal plates of the frontal, ventral and marginal cirri, to each of which are attached the dissociated fibers (c). By means of microdissection needles, Taylor demonstrated that these fibers have nothing to do with the maintenance of body form since there results no deformity when *Euplotes* is cut fully two-thirds its width, thus cutting the fibers, and that when the motorium is destroyed or its attached fibers are cut, there is no coördination in the movements of the adoral membranellae and anal cirri. Turner (1933) however is inclined to think that there is no motorium in this protozoan.

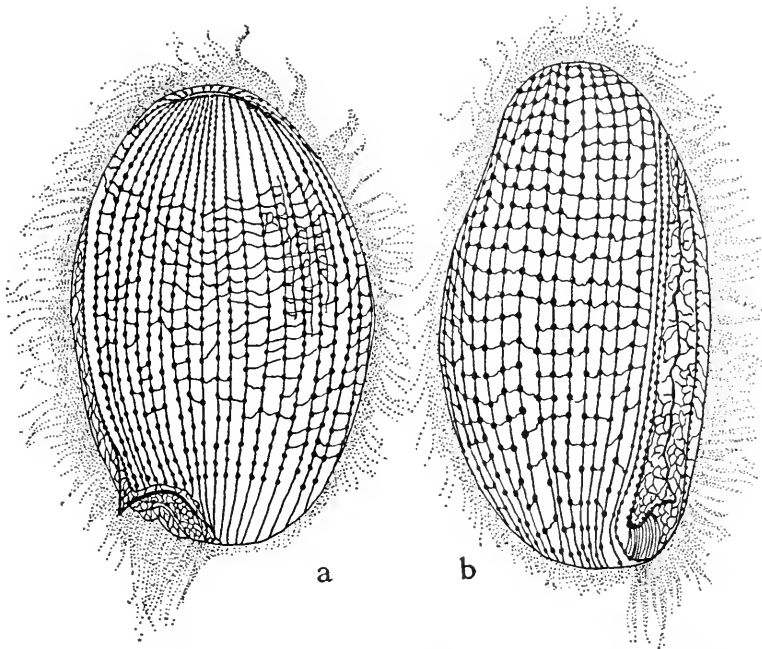


FIG. 18. The silverline system of *Ancistruma mytili*, $\times 1000$ (Kidder).
a, ventral view; b, dorsal view.

A striking feature common to all neuromotor systems, is that there seems to be a central motorium from which radiate fibers to different ciliary structures and that, at the bases of such motor organellae, are found the basal granules or plates to which the "nerve" fibers from the motorium are attached.

Independent of the studies on the neuromotor system of American investigators, Klein (1926) introduced the silver-impregnation method which had first been used by Golgi in 1873 to demonstrate various fibrillar structures of metazoan cells, to Protozoa in order to demonstrate the cortical fibers present in ciliates, by dry-fixation and impregnating with silver nitrate. Klein (1926-1930) subjected the ciliates of numerous genera and species to this method, and observed that there was a fibrillar system in the ectoplasm at the level of the basal granules which cannot be demonstrated by other methods. Klein (1927) named the fibers **silver lines** and the whole complex, the **silverline system**, which is characteristic of each species (Fig. 18). Chatton

and Lwoff, Gelei, Jírovec, Lynch, Jacobson, Kidder, Lund, and others, applied the silver-impregnation methods to many other ciliates and confirmed Klein's observations. Chatton and Lwoff (1935) found in *Apostomea*, the system remains even after the embryonic cilia have entirely disappeared and, therefore, named it *infraciliature*.

The question whether the neuromotor apparatus and the silver-line system are independent structures or different aspects of the same structure has been raised frequently. Turner (1933) found that in *Euplotes patella* the silverline system is a regular latticework on the dorsal surface and a more irregular network on the ventral surface. These lines are associated with rows of rosettes from which bristles extend. These bristles are held to be sensory in function and the network, a sensory conductor system, which is connected with the neuromotor system. Turner maintains that the neuromotor apparatus in *Euplotes patella* is augmented by a distinct but connected external network of sensory fibrils.

Lund (1933) also made a comparative study of the two systems in *Paramecium multimicronucleata*, and observed that the silver-line system of this ciliate consists of two parts. One portion is made up of a series of closely-set polygons, usually hexagons, but flattened into rhomboids or other quadrilaterals in the regions of the cytostome, cytopyge, and sutures. This system of lines stains if the organisms are well dried. Usually the lines appear solid, but frequently they are interrupted to appear double at the vertices of the polygons which Klein called "indirectly connected" (pellicular) conductile system. In the middle of the anterior and posterior sides of the hexagons is found one granule or a cluster of 2-4 granules, which marks the outer end of the trichocyst. The second part which Klein called "directly connected" (subpellicular) conductile system consists essentially of the longitudinal lines connecting all basal granules in a longitudinal row of hexagons and of delicate transverse fibrils connecting granules of adjacent rows especially in the cytostomal region (Fig. 19).

By using Sharp's technique, Lund found the neuromotor system of *Paramecium multimicronucleata* constructed as follows: The subpellicular portion of the system is the longitudinal fibrils which connect the basal granules. In the cytostomal region, the fibrils of right and left sides curve inward forming complete circuits (the circular cytosomal fibrils) (Fig. 20). The postoral

suture is separated at the point where the cytopye is situated. Usually 40–50 fibrils radiate outward from the cytostome (the radial cytostomal fibrils). The pharyngeal portion is more complex and consists of 1) the oesophageal network, 2) the motorium and associated fibrils, 3) penniculus which is composed of 8 rows of basal granules, thus forming a heavy band of cilia in the

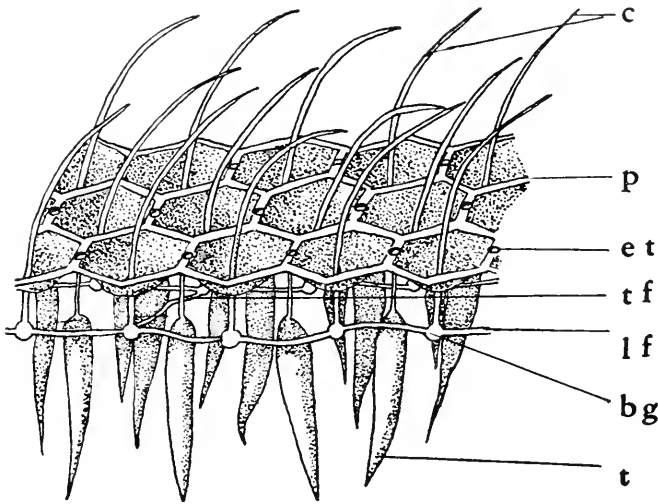


FIG. 19. Diagram of the cortical region of *Paramecium multimicronucleata*, showing various organelles, $\times 7300$ (Lund). bg, basal granule; c, cilia; et, tip of trichocyst; lf, longitudinal fibril; p, pellicle; t, trichocyst; tf, transverse fibril.

cytopharynx, 4) oesophageal process, 5) paraoesophageal fibrils, 6) posterior neuromotor chain, and 7) postoesophageal fibrils. Lund concludes that the so-called silverline system includes three structures: namely, the peculiarly ridged pellicle; trichocysts which have no fibrillar connections among them or with fibrils, hence not conductile; and the subpellicular system, the last of which is that part of the neuromotor system that concerns with the body cilia. ten Kate (1927) suggested that **sensomotor apparatus** is a better term than the neuromotor apparatus.

Protective or supportive organelles

The external structures as found among various Protozoa which serve for body protection have already been considered

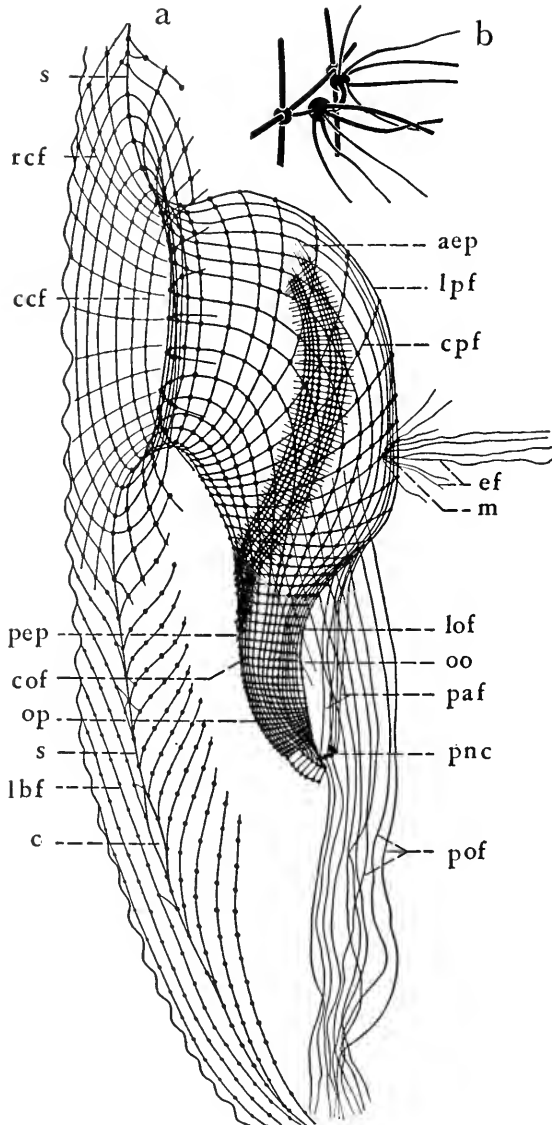


FIG. 20. The neuromotor system of *Paramecium multimicronucleata* (Lund). a, oral network; b, motorium, $\times 1670$. aep, anterior end of penniculus; c, cytophyge; ccf, circular cytotosomal fibril; cof, circular oesophageal fibril; cpf, circular pharyngeal fibril; ef, endoplasmic fibrils; lbf, longitudinal body fibril; lof, longitudinal oesophageal fibrils; lpf, longitudinal pharyngeal fibril; m, motorium; oo, opening of oesophagus; op, oesophageal process; paf, paraesophageal fibrils; pep, posterior end of penniculus; pnc, posterior neuromotor chain; pof, postoesophageal fibrils; rcf, radial cytotosomal fibril; s, suture.

(p. 38). Here certain internal structures will be discussed. The greater part of the shell of Foraminifera is to be looked upon as endoskeleton and thus supportive in function. In Radiolaria, there is a membranous structure, the **central capsule**, which divides the body into a central region and a peripheral zone. The intracapsular portion contains the nucleus or nuclei, and is the seat of reproductive processes, and thus the capsule is to be considered as a protective organella. The endoskeletal structures of Radiolaria vary in chemical composition and forms, and are arranged with a remarkable regularity (pp. 371-376).

In some of the astomous euciliates, there are certain structures which seem to serve for attaching the body to the host's organ, but which seem to be supportive to a certain extent also. The peculiar organella, furcula, observed by Lynch in Lechriopyla (p. 536) is said to be concerned with either the neuromotor system or protection. The members of the family Ophryoscolecidae, which are common commensals of the stomach of ruminants, have conspicuous **endoskeletal plates** which arise in the oral region and extend posteriorly. Dogiel (1923) believed that the skeletal plates of Cycloposthium and Ophryoscolecidae are made up of hemicellulose, "ophryoscolecine," which was also observed by Strelkow (1929). MacLennan found that the skeletal plates of *Polyplastron multivesiculatum* were composed of small, roughly prismatic blocks of glycogen, each possessing a central granule.

In certain Polymastigina and Hypermastigina, there occurs a flexible structure known as the **axostyle**, which varies from a filamentous structure as in several Trichomonas, to a very conspicuous rod-like structure occurring in Parajoenia, Gigantomonas, etc. The anterior end of the axostyle is very close to the anterior tip of the body, and it extends lengthwise through the cytoplasm, ending near the posterior end or extending beyond the body surface. In other cases, the axostyle is replaced by a bundle of **axostylar filaments** which have connections with the flagella as seen in Polymonadina and certain Hypermastigina such as Lophomonas. Kirby showed that in *Trichomonas termopsidis*, the axostyle and the granules occurring in it, are of glycogenous substance.

In trichomonad flagellates there is often present along the attachment of the undulating membrane a rod-like structure which has been known as **costa** (Kunstler) and which, according to

Kirby's extensive study, appears to be the most highly developed in *Pseudotrypanosoma* and *Trichomonas*. The staining reaction indicates that its chemical composition is different from that of flagella, blepharoplast, parabasal body, or chromatin.

In the gymnostomous ciliates, the cytopharynx is often surrounded by rod-like bodies, and the entire apparatus is often called **oral** or **pharyngeal basket**, which is considered as supportive in function. The rod-like bodies appear in most cases to

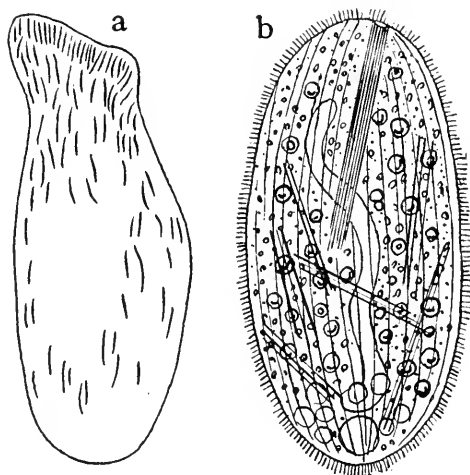


FIG. 21. a, trichites in *Spathidium spathula*, $\times 300$ (Woodruff and Spencer); b, trichites in *Enchelyodon farctus*, $\times 400$ (Roux).

be trichites which may have been derived from the trichoeysts, but which do not explode as do the latter. For example, in *Chilodonella cucullulus* the oral basket is composed of 12 trichites which are so completely fused in part that the lower portion appears as a smooth tube and in *Enchelyodon farctus* (Fig. 21, b) much longer trichites form the basket, with reserve structures scattered throughout the cytoplasm (Engelmann). In *Spathidium spathula* (Fig. 21, a), trichites are imbedded like a paling in the thickened rim of the anterior end. They are also distributed throughout the endoplasm and, according to Woodruff and Spencer, "some of these are apparently newly formed and being transported to the oral region, while others may well be trichites which have been torn away during the process of prey ingestion."

Whether the numerous 12–20 μ long needle-like endoskeletal structures which Kahl observed in *Remanella* (p. 522) are modified trichites or not, is not known.

In numerous ciliates, there is another ectoplasmic organelle, the **trichocyst**, which is much shorter, though somewhat similar in general form. As seen in a *Paramecium*, the refractile fusiform trichocysts are embedded in the ectoplasm and arranged at right angles to the body surface, while in forms, such as *Cyclogramma* they are situated obliquely (Fig. 240, *c*). In *Frontonia leucas* (Fig. 22), Tönniges found that the trichocysts originated in the chromatinic endosomes of the macronucleus and development takes place during their migration to the ectoplasm; on the other hand, Brodsky believes that the trichocysts are composed of colloidal excretory substances and are first formed in the vicinity of the macronucleus, becoming fully formed during the course of their migration toward the periphery of the body. In species of *Prorodon*, Krüger recently observed that the rod-like trichocysts of these ciliates are composed of a cylindrical sac containing a long filament which is arranged in a manner somewhat similar to the polar capsule of endosporidian spores. The end facing the body surface is filamentous and connected with the pellicle.

The extrusion of the trichocysts is easily induced by means of mechanical pressure or chemical (acid or alkaline) stimulation, though the mechanism of extrusion is not well understood in all forms. Brodsky maintains that the fundamental force is not the mechanical pressure, but that the expansion of the colloidal substances results under the influence of certain stimuli in the extrusion of the trichocysts through the pellicle. The fully extruded trichocysts are needle-like in general form. The trichocysts of *Frontonia leucas* are about 6 μ long, but when extruded, measure 50–60 μ in length, and those of *Paramecium caudatum* may reach 40 μ in length.

Dileptus anser feeds on various ciliates through the cytostome, located at the base of the proboscis, which possesses a band of long trichocysts on its ventral side. When food organisms come in contact with the ventral side of the proboscis, they give a violent jerk, and remain motionless. Visser saw no formed elements discharged from the trichocysts, and, therefore, considered that these trichocysts contained a toxic fluid and named them toxicytes. Recently Hayes found that the exploded trichocysts (Fig.

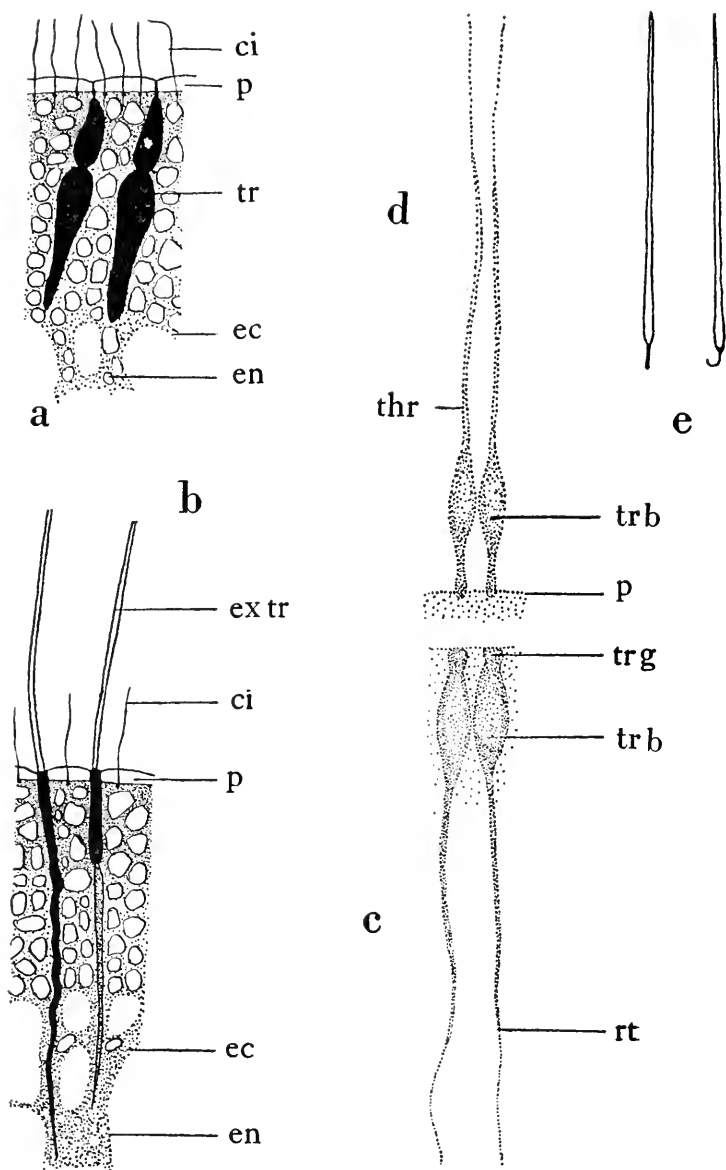


FIG. 22. a, b, cortical region of *Frontonia leucas*, with embedded and extruded trichocysts (Tönniges); c, d, embedded and discharged trichocysts of *Dileptus anser*, $\times 4200$ (Hayes); e, two extruded trichocysts of *Paramecium caudatum*, $\times 1530$. ci, cilium; ec, ectoplasm; en, endoplasm; extr, extruded trichocyst; p, pellicle; rt, root of trichocyst; thr, thread of trichocyst; tr, trichocyst; trb, bulb of trichocyst; trg, trichocyst granule.

22) could be distinctly seen and suggested that these trichocysts themselves may be toxic.

Although the trichocyst was first discovered by Ellis (1769) and so named by Allman (1855), nothing concrete is yet known as to their function. Ordinarily the trichocysts are considered as a defensive organella as in the case of the oft-quoted example *Paramecium*, but, as Mast demonstrated, the extruded trichocysts of this ciliate do not have any effect upon *Didinium* other than forming a viscid mass about the former to hamper the latter. Penard considers that some trichocysts may be secretory organellae to produce material for loricae or envelope, with which view Kahl concurs, as granular to rod-shaped trichocysts occur in *Metopus*, *Amphileptus*, etc. Klein has called these ectoplasmic granules **protrichocysts**, and in *Prorodon*, Krüger observed, besides typical tubular trichocysts, torpedo-like forms to which he applied the same name. To this group may belong the trichocysts recognized by Kidder in *Conchophthirus mytili*. The trichocysts present in certain Cryptomonadina (*Chilomonas* and *Cyathomonas*) are probably homologous with the protrichocysts. The pigments, which give a beautiful coloration to certain ciliates such as *Stentor* and *Blepharisma*, are said to be lodged in the protrichocysts.

Hold-fast organellae

In the Mastigophora, Ciliophora, and a few Sarcodina, there are forms which possess a **stalk** supporting the body or the lorica. With the stalk the organism is attached to a solid surface. In some cases, as in *Anthophysa*, *Maryna*, etc., the dendritic stalks are made up of gelatinous substances rich in iron, which gives to it a reddish color. In parasitic Protozoa, there are special organellae developed for attachment. Many genera of cephaline gregarines are provided with an **epimerite** of different structures (Figs. 181–183), by which the organisms are able to attach themselves to the gut epithelium of the host. In Astomata, such as *Intoshellina*, *Maupasella*, *Lachmannella*, etc., simple or complex protrusible chitinous structures are often present in the anterior region; or a certain area of the body may be concave and serves for adhesion to the host, as in *Rhizocaryum*, *Perezella*, etc.; or, again, there may be a distinctive sucker-like organella near the anterior extremity of the body, as in *Haptophyra*, *Steinella*, etc. A sucker is also present on the antero-ventral part of *Giardia intestinalis*.

In the Myxosporidia and Actinomyxidia, there appear, during the development of spore, 1-4 special cells which develop into 1-4 **polar capsules**, each, when fully formed, enclosing a more or less long spirally coiled hollow thread, the **polar filament** (Fig. 221). The polar filament is considered as a temporary anchoring organella of the spore at the time of its germination after it gained entrance into the alimentary canal of a suitable host. The **nematocysts** (Fig. 104, *b*) of certain dinoflagellates belonging to *Nematoidium* and *Polykrikos*, are almost identical in structure with those found in the coelenterates. They are distributed through the cytoplasm, and various developmental stages were noticed by Chatton, and Kofoid and Swezy, which indicates that they are characteristic structures of these dinoflagellates and not foreign in origin as had been held by some. The function of the nematocysts in these protozoans is not understood.

The parabasal apparatus

In the cytosome of many parasitic flagellates, there is frequently present a conspicuous structure known as the **parabasal apparatus** (Janicki), consisting of the parabasal body and the thread (Cleveland), which latter may be absent in some cases. This structure varies greatly among different genera and species in appearance, structure and position within the body. It is usually connected with the blepharoplast and located very close to the nucleus, though not directly connected with it. It may be single, double, or multiple, and may be pyriform, straight or curved rod-like, bandform, spirally coiled or collar-like (Fig. 23). Kofoid and Swezy considered that the parabasal body is derived from the nuclear chromatin, varies in size according to the metabolic demands of the organism, and is a "kinetic reservoir." On the other hand, Duboseq and Grassé maintain that this body is the Golgi apparatus, since 1) acetic acid destroys both the parabasal body and the Golgi apparatus; 2) both are demonstrable with the same technique; 3) the parabasal body is made up of chromophile and chromophobe parts as is the Golgi apparatus; and 4) there is a strong evidence that the parabasal body is secretory in function. According to Kirby, who has made an extensive study of this organella, the parabasal body could be stained with Delafield's haematoxylin or Mallory's triple stain after fixation with acetic acid-containing fixatives and the body does not show

any evidence to indicate that it is a secretory organella. Moreover the parabasal body is discarded or absorbed at the time of division of the body and two new ones are formed.

In the parabasal body of *Lophomonas blattarum* to which the name was originally applied, the structure is discarded when the organism divides and two new ones are reformed from the centriole or blepharoplast (Fig. 59), and its function appears to be

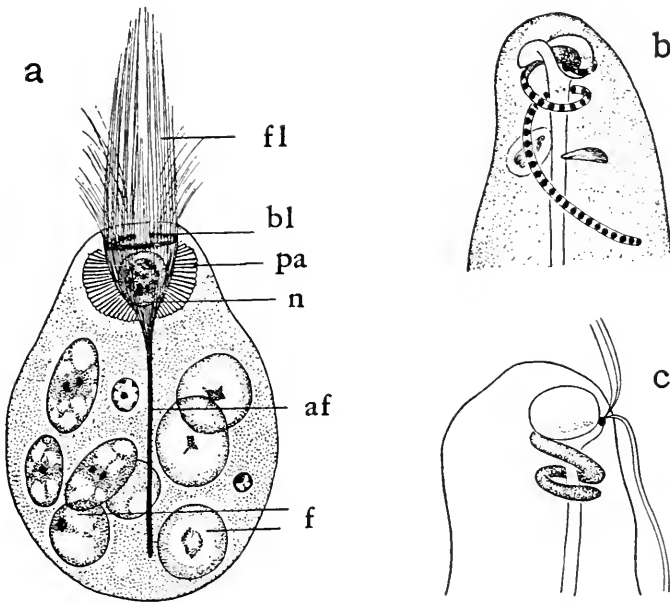


FIG. 23. Parabasal apparatus in: a, *Lophomonas blattarum* (Kudo); b, *Metaderescorina debitis*; c, *Derescorina* sp. (Kirby). af, axostylar filaments; bl, blepharoplast; f, food particles; fl, flagella; n, nucleus; pa, parabasal apparatus.

supportive. Possibly not all so-called parabasal bodies are homologous or analogous and a fuller comprehension of the function of the organella rests with further investigations.

The blepharoplast or centriole

In the Mastigophora or in other groups in which flagellate stages occur, the flagellum ends internally in a **basal granule**, which, in turn, is sometimes connected by a much larger body. This latter organella has been called the **centriole** or blepharo-

plast. In many instances they appear to be combined in one. The blepharoplast is further connected by a fibril, the **rhizoplast**, with the nucleus (Fig. 24). The blepharoplast and centriole are con-

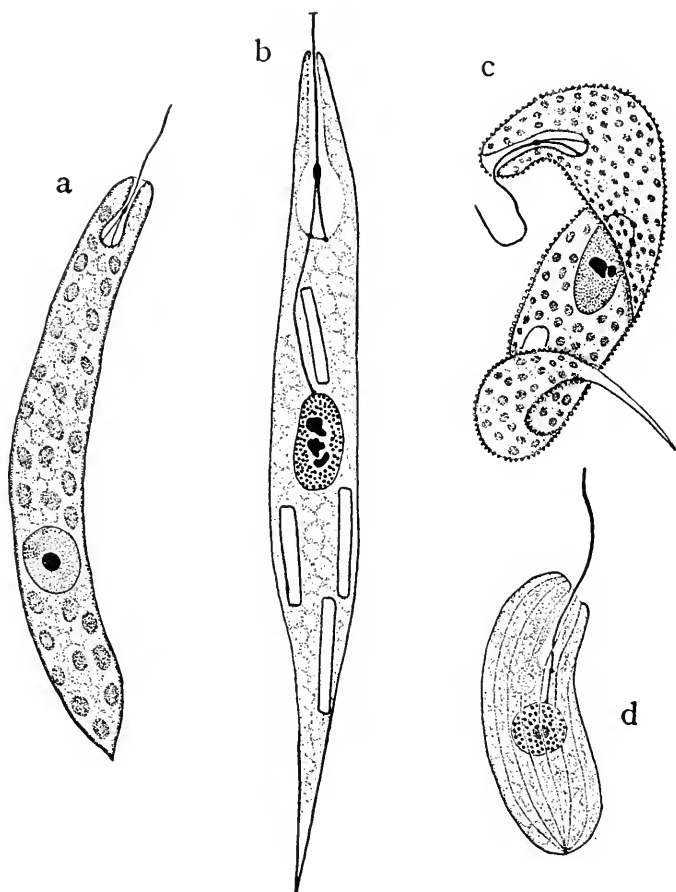


FIG. 24. Flagellar attachment in Euglenoidina (Hall and Jahn). a, *Euglena deses*, $\times 2025$; b, *E. acus*, $\times 750$; c, *E. spirogyra*, $\times 720$; d, *Menoidium incurvum*, $\times 1550$.

sidered synonymous by Minchin, Cleveland, and others, since this organella gives rise to the kinetic element. Woodcock and Minchin held, on the other hand, that the blepharoplast was a nucleus holding a special relation with locomotor organellae, and

called it **kinetonucleus**. In recent years it has become known that the blepharoplast of many flagellates responds positively to Feulgen's nucleal reaction which indicates the presence of thymonucleic acid or chromatin in this structure.

The Golgi apparatus

With the discovery of a wide distribution of the so-called Golgi apparatus in metazoan cells, a number of protozoologists also reported a homologous structure from many protozoans. It seems impossible at present to indicate just exactly what is the Golgi

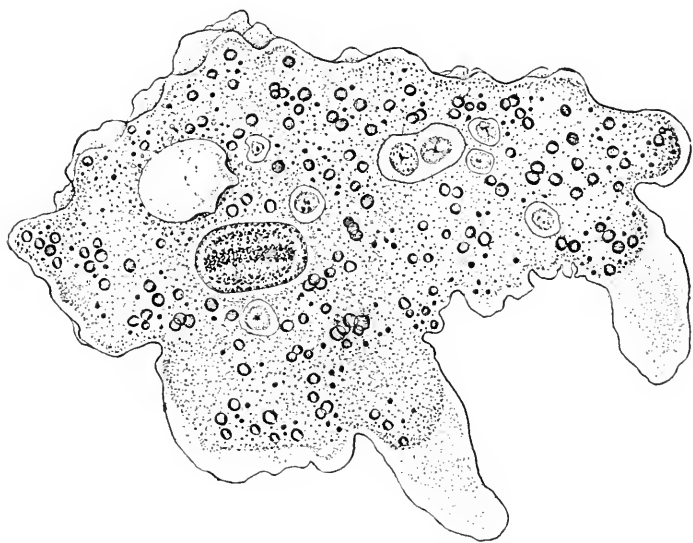


FIG. 25. The Golgi bodies in *Amoeba proteus* (Brown).

apparatus, since the so-called Golgi techniques, the important ones of which are based upon the assumption that the Golgi material is osmiophile and argentophile, and possesses a strong affinity to neutral red, are not specific and the results obtained by using the same method often vary a great deal. Some of the examples of the Golgi apparatus reported from various Protozoa are mentioned on page 70.

It appears thus that the Golgi bodies occurring in Protozoa are small osmiophilic granules or larger spherules which are composed of osmiophile cortical and osmiophobe central substances. Fre-

Protozoa	Golgi apparatus	Observers
Monocystis, Gregarina	Spheres, rings, crescents	Hirschler
<i>Endamoeba blattae</i>	Spheres, rings, crescents	Hirschler
Adelea	Crescents, beaded grains	King and Gatenby
<i>Entamoeba gingivalis</i>	Rings, crescents to network	Causey
Vorticella, Lionotus, Paramecium, Dogi- ella, Nassula, Chilo- monas, Chilodonella	The membrane of con- tractile vacuole and col- lecting canals	Nassonov
Holomastigotes, Pyr- sonympha, etc.	Parabasal bodies	Dubocsq and Grassé
Aggregata, gregarines	Crescents, rings	Joyet- Lavergne
Euglenoidina	Stigma	Grassé
Chilomonas	Granules, vacuoles	Hall
Peranema	Rings, globules, granules	Hall
Chromulina, Astasia	Rings, spherules with a dark rim	Hall
<i>Amoeba proteus</i> (Fig. 25)	Rings, crescents, globules, granules	Brown
Pyrsonympha, Di- nenympha	Rings, crescents, spherules; granules break down to form network near pos- terior end	Brown
<i>Euglena gracilis</i>	Spherical, discoidal with dark rim; tend to group around or near nucleus	Brown
<i>Blepharisma undulans</i>	Rings in the cytoplasm	Moore

quently the cortical layer is of unequal thickness, and, therefore, crescentic forms appear. Ringform apparatus was noted in Chilodonella and Dogiella by Nassonov and network-like forms were observed by Brown in Pyrsonympha and Dinenympha. The numerous observations on the Golgi apparatus of Protozoa as well as of Metazoa, indicate that it is composed of a lipoidal material in combination with a protein.

In line with the suggestion made for the metazoan cell, the Golgi apparatus of Protozoa is considered as having something to do with secretion or excretion. Nassonov considers that osmiophilic lipoidal substance, which he observed in the neighborhood of the walls of the contractile vacuole and its collecting canals in many ciliates and flagellates, is homologous with the meta-

zoan Golgi apparatus and secretes the fluid waste material into the vacuole from which it is excreted to the exterior. According to Brown, there is no blackening by osmic impregnation of the contractile vacuole in *Amoeba proteus*, but fusion of minute vacuoles associated with crescentic Golgi bodies produces the vacuole.

Duboseq and Grassé who hold that the parabasal body is the Golgi apparatus, maintain that this body is a source of energy which is utilized by the motor organellae. Joyet-Lavergne pointed out that in certain sporozoans the Golgi apparatus is granular and may be the center of enzyme production. The exact morphological and physiological information of the Golgi apparatus must be looked for in future observations.

The chondriosomes

Widely distributed in many metazoan cells, the chondriosomes have also been recognized in various Protozoa. The chondriosomes possess a low refractive index, and are composed of substances easily soluble in alcohol, acetic acid, etc. Janus green B stains them even in 1:500,000 solution, but stains also other inclusions, such as the Golgi bodies (in some cases) and certain bacteria. According to Horning (1926), janus red is said to be a more exclusive chondriosome stain, as it does not stain bacteria. The chemical composition of the chondriosome seems to be somewhat similar to that of the Golgi body; namely, it is a protein compounded with a lipoidal substance. If the protein is small in amount, it is said to be unstable and easily attacked by reagents; on the other hand, if the protein is relatively abundant, it is more stable and resistant to reagents.

The chondriosomes occur as small spherical to oval granules, rod-like or filamentous bodies, and show a tendency to adhere to or remain near protoplasmic surfaces. In many cases they are distributed without any definite order; in others, as in *Paramecium* or *Opalina*, they are regularly arranged between the basal granules of cilia (Horning). In *Peranema trichophorum* (Fig. 26), according to Hall, the chondriosomes are said to be located along the spiral striae of the pellicle. Causey (1925) noticed in *Leishmania brasiliensis* usually eight spherical chondriosomes in each individual, which become rod-shaped when the organism divides. He further observed spherical and rod-like chondriosomes in *Noctiluca scintillans*.

In certain Protozoa, the chondriosomes are not always demonstrable. For example, Horning states in *Monocystis* the chondriosomes present throughout the asexual life-cycle as rod-shaped bodies, but at the beginning of the spore formation they decrease in size and number, and in the spore none exists. The chondriosomes appear as soon as the sporozoites are set free. Thus it would appear that the chondriosomes were reformed *de novo*. On the other hand, Fauré-Fremiet, the first student of the chondriosomes in Protozoa, maintained that they reproduce by division,

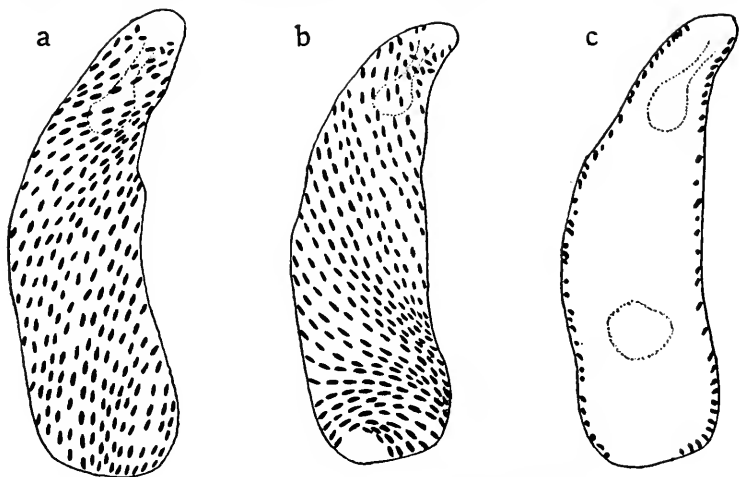


FIG. 26. The chondriosomes in *Peranema trichophorum*, $\times 1750$ (Hall).
a, b, surface views and c, optical section of a single individual.

which has since been confirmed by many observers. As a matter of fact, Horning found in *Opalina*, the chondriosomes are twisted filamentous structures and underwent multiple longitudinal fission in asexual division phase. Before encystment, the chondriosomes divide repeatedly transversely and become spherical bodies which persist during encystment and in the gametes. In zygotes, these spherical bodies fuse to produce longer forms which break up into elongate filamentous structures. Richardson and Horning further succeeded in bringing about division of the chondriosomes in *Opalina* by changing pH of the medium.

As to the function of chondriosomes, opinions vary. A number of observers hold that they are concerned with the digestive process. After studying the relationship between the chondrio-

somes and food vacuoles of *Amoeba* and *Paramecium*, Horning suggested that the chondriosomes are the seat of enzyme activity and it is even probable that they actually give up their own substance for this purpose. The view that the chondriosomes may have something to do with the cell-respiration expressed by Kingsbury was further elaborated by Joyet-Lavergne through his studies on certain Sporozoa. That the chondriosomes are actively concerned with the development of the gametes of the Metazoa is well known. Zweibaum's observation, showing an increase in the amount of fatty acid in *Paramecium* just prior to conjugation, appears to suggest this function. On the other hand, Calkins found that in *Uroleptus*, the chondriosomes became abundant in exconjugants, due to transformation of the macronuclear material into the chondriosomes. It may be stated that the chondriosomes appear to be associated with the formation of enzymes which participate actively in the processes of catalysis or synthesis in the protozoan body. The author agrees with McBride and Hewer who wrote: "it is a remarkable thing that so little is known positively about one of the 'best known' protoplasmic inclusions."

The contractile and other vacuoles

The majority of Protozoa possess one or more vacuoles known as pulsating or **contractile vacuoles**. They occur regularly in all freshwater inhabiting Sarcodina and Mastigophora, and in Ciliophora regardless of habitat. In the Sporozoa, which are all parasitic, and the Sarcodina and Mastigophora, which live either in salt water or in the body of other animals, there is no contractile vacuole.

In various species of free-living amoebae, the contractile vacuole is formed by accumulation of water in one or more droplets which finally fuse into one. It enlarges itself continuously until it reaches a maximum size (*diastole*) and suddenly bursts through the thin cytoplasmic layer above it (*systole*), discharging its contents to outside. The location of the vacuole is not definite in such forms and, therefore, it moves about with the cytoplasmic movements; and, as a rule, it is confined to the temporary posterior region of the body. Although almost spherical in form, it may occasionally be irregular in shape, as in *Amoeba striata* (Fig. 140, *f*). In many testaceans and heliozoans, the contractile vacuoles

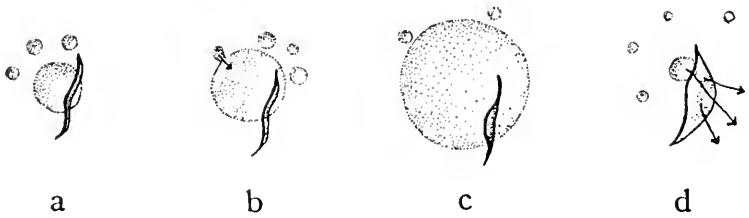


FIG. 27. Diagrams showing the contractile vacuole, the accessory vacuoles and the aperture, during diastole and systole in *Conchophthirus* (Kidder).

which are variable in number, are formed in the ectoplasm and the body surface bulges out above the vacuoles at diastole.

In the *Mastigophora*, the contractile vacuole appears to be more or less constant in position. In *Phytomastigina*, they are usually located near the anterior region and, in *Zoomastigina*, as a rule, in the posterior half of the body. The number of the vacuoles present in an individual varies from one to several. In *Euglenoidina*, one or more vacuoles are sometimes arranged near the reservoir which opens to "cytopharynx."

In the *Ciliophora*, except *Protociliata*, there occur one to many contractile vacuoles, which seem to be located in the deepest part of the ectoplasm and therefore constant in position. Directly above each vacuole is found a pore in the pellicle, through which the contents of the vacuole are discharged to outside. In the species of *Conchophthirus*, Kidder (1934) observed a narrow slit in the pellicle just posterior to the vacuole on the dorsal surface (Fig. 27). The margin of the slit is thickened and highly refractile. During diastole, the slit is nearly closed and, at systole, the wall of the contractile vacuole appears to break and the slit opens suddenly, the vacuolar contents pouring out slowly. When there is only one contractile vacuole, it is usually located either near the cytopharynx or, more often, in the posterior part of the body. When several to many vacuoles are present, they may be distributed without apparent order, in linear series, or along the body outline. When the contractile vacuoles are deeply seated, there is a delicate duct which connects the vacuole with the pore on the pellicle as in *Paramecium woodruffi* or in *Ophryoscolecidae*. In *Balantidium*, *Nyctotherus*, etc., the contractile vacuole is formed very close to the permanent cytopyge located at the posterior extremity, through which it empties its contents.

In a number of ciliates there occur radiating or **collecting canals** besides the main contractile vacuole. These canals radiate from the central vacuole in *Paramecium*, *Frontonia*, *Disemastoma*, etc. But when the vacuole is terminal, the collecting canals of course do not radiate, in which case the number of the canals varies among different species: one in *Spirostomum*, *Stentor*, etc., 2 in *Climacostomum*, *Eschaneustyla*, etc., and several in *Tillina*. In *Peritricha*, the contractile vacuole occurs near the posterior region of the peristome and its contents are discharged through a canal into the vestibule.

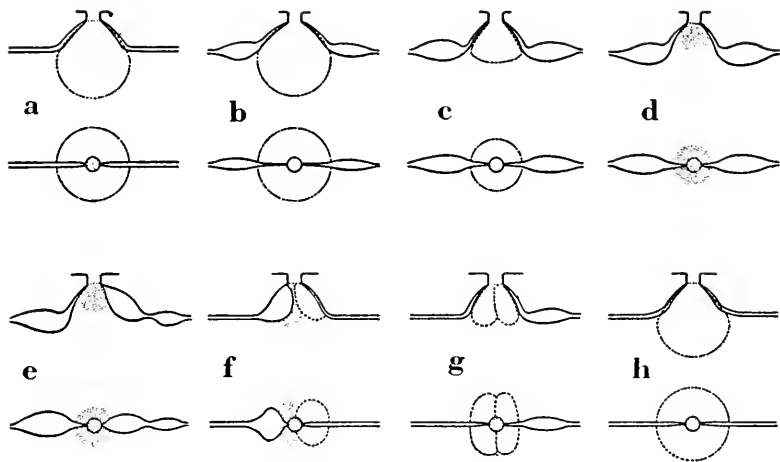


FIG. 28. Diagrams showing the successive stages in the formation of the contractile vacuole in *Paramecium multimicronucleata* (King); upper figures are side views; lower figures front views; solid lines indicate permanent structures; dotted lines temporary structures. a, full diastole; b-d, stages of systole; e, contents of ampulla passing into injection canal; f, formation of vesicles from injection canals; g, fusion of vesicles to form contractile vacuole; h, full diastole.

Of numerous observations concerning the operation of the contractile vacuole, that of King (1935) on *Paramecium multimicronucleata* (Figs. 28, 29) may be quoted here. In this ciliate, there are 2 to 7 contractile vacuoles which are located below the ectoplasm on the aboral side. There is a permanent pore above each vacuole. Leading to the pore is a short tube-like invagination of the pellicle, with inner end of which the temporary membrane of the vacuole is in contact (Fig. 28, a). Each vacuole has 5-10 long

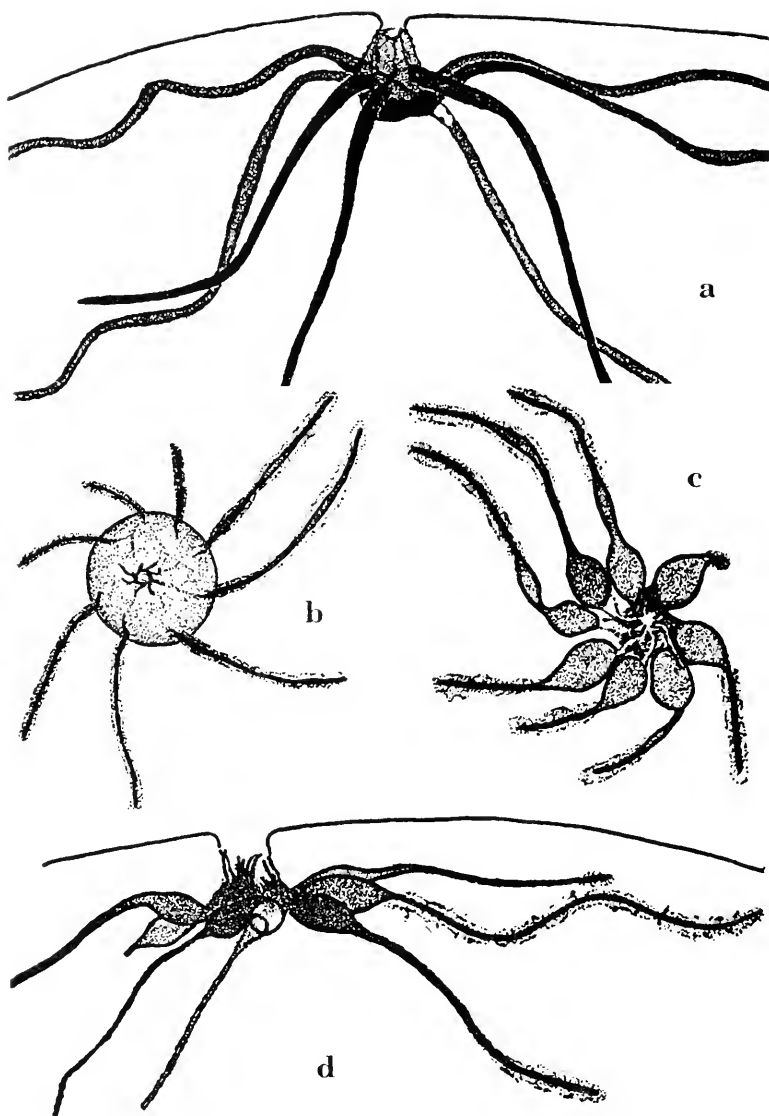


FIG. 29. Contractile vacuoles of *Paramecium multimicronucleata*, $\times 1200$ (King). a, early systole, side view; b, diastole, front view; c, complete systole, front view; d, systole, side view.

collecting canals with strongly osmiophile walls (Fig. 29), and each canal is made up of terminal portion, a proximal injection canal, and an ampulla between them. Surrounding the distal portion, there is osmiophilic cytoplasm which may be granulated or finely reticulated, and which Nasonov interpreted as homologous to the Golgi apparatus of the metazoan cell. The injection canal extends up to the pore. The ampulla becomes distended first with fluid transported discontinuously down the canal and the fluid next moves into the injection canal. The fluid now is expelled into the cytoplasm just beneath the pore as a vesicle, the membrane of which is derived from a membrane which closed the end of the injection canal. These fluid vesicles coalesce presently to form the contractile vacuole in full diastole and the fluid is discharged to exterior through the pore, which becomes closed by the remains of the membrane of the discharged vacuole. The function of the contractile vacuole is considered in the following chapter (p. 98).

Various other vacuoles or vesicles occur in different Protozoa. In the ciliates belonging to Loxodidae, there are variable numbers of **Müller's vesicles** or bodies arranged in 1-2 rows along the aboral surface. These vesicles (Fig. 30, *a-c*) vary in diameter from 5 to 8.5μ and contain a clear fluid in which one large spherule or several small highly refractile spherules are suspended. In some, there is a filamentous connection between the spherules and the wall of the vesicle. Penard maintains that these bodies are balancing cell-organs and called the vesicle, the statocyst, and the spherules, the statoliths.

Another vacuole, known as **concrement vacuole**, is a characteristic organella in Butschliidae and Paraisotrichidae. As a rule, there is a single vacuole present in an individual at the anterior third of body. It is spherical to oval and its structure appears to be highly complex. According to Dogiel, the vacuole is composed of a pellicular cap, a permanent vacuolar wall, concretment grains and two fibrillar systems (Fig. 30, *d*). When the organism divides, the anterior daughter individual retains it, and the posterior individual develops a new one from the pellicle into which concretment grains enter after first appearing in the endoplasm. This vacuole shows no external pore. Dogiel believes that its function is sensory and has named the vacuole, the statocyst, and the enclosed grains, the statoliths.

Food vacuoles are conspicuously present in the holozoic Pro-

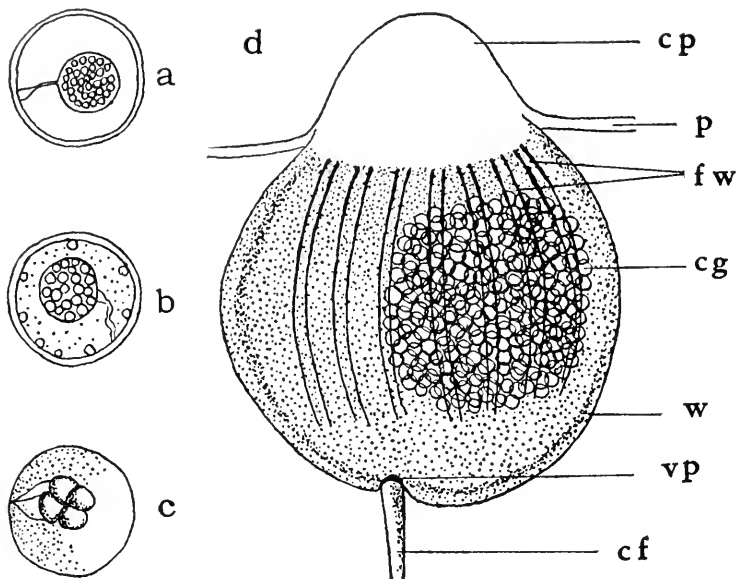


FIG. 30. a-c, Müller's vesicles in *Loxodes* (a, b) and in *Remanella* (c) (a, Penard; b, c, Kahl); d, concrement vacuole of *Blepharoprosthium* (Dogiel). cf, centripetal fibril; cg, concrement grains; cp, cap; fw, fibrils of wall; p, pellicle; vp, vacuolar pore; w, wall.

tozoa which take in whole or parts of other organisms as food. The food vacuole is a space in the cytoplasm, containing the fluid medium which surrounds the protozoans and in which are suspended the food matter, such as various *Protophyta*, other *Protozoa* or small *Metazoa*. In the *Sarcodina*, the *Mastigophora* and the *Suctoria*, which do not possess a cytostome, the food vacuoles assume the shape of the food particles and, when these particles are large, it is difficult to make out the thin film which surrounds them. When minute food particles are taken through a cytostome, as is the case with the majority of *euciliates*, the food vacuoles are usually spherical and of approximately the same size within a single protozoan. In the *saprozoic Protozoa*, which absorb fluid substances through the body surface, food vacuoles containing solid food, of course, do not occur.

The chromatophore and associated organellae

In the *Phytomastigina* and certain other forms which are green-colored, one to many **chromatophores** (Fig. 31) or chloroplasts containing chlorophyll occur in the cytosome. The chroma-

tophores vary in form among different species; namely, discoidal, ovoid, band-form, rod-like, cup-like, network or irregularly diffused. The color of the chromatophore depends upon the amount and kinds of pigment which envelops the underlying chlorophyll substance. Thus the chromatophores of Chrysomonadina are brown or orange, as they contain one or more accessory pigments, including phycochrysin, and those of Cryptomonadina are of various types of brown with very diverse pigmentation. In Chloromonadina, the chromatophores are bright green, containing an excess of xanthophyll. In dinoflagellates, they are dark yellow or brown, because of the presence of pigments: carotin, phyloxanthin, and peridinin (Kylin), the last of which is said to give the brown coloration. A few species of Gymnodinium contain blue-green chromatophores for which phycocyanin is held to be responsible. The chromatophores of Phytomonadina and Euglenoidina are free from any pigmentation, and therefore green. Aside from various pigments associated with the chromatophores, there are carotinoid pigments which occur often outside the chromatophores, and are collectively known as **haematochrome**. The haematochrome occurs in *Haematococcus pluvialis*, *Euglena sanguinea*, *Chlamydomonas*, etc. In *Haematococcus*, it increases in volume and in intensity when there is a deficiency in phosphorus and especially in nitrogen; and when nitrogen and phosphorus are sufficiently present in the culture medium, the haematochrome loses its color completely (Reichenow; Pringsheim). Steinecke also noticed that the frequent yellow coloration of phytomonads in moorland pools is due to a development of carotin in the chromatophores as a result of deficiency in nitrogen.

In association with the chromatophores are found the **pyrenoids** (Fig. 31) which are usually embedded in them. The pyrenoid is a viscous structureless mass of protein (Czurda), and may or may not be covered by tightly fitting starch-envelope, composed of several pieces or grains which appear to grow by apposition of new material on the external surface. A pyrenoid divides when it reaches a certain size, and also at the time of the division of the organism in which it occurs. As to its function, it is generally agreed that the pyrenoid is concerned with the formation of the starch and allied anabolic products of photosynthesis.

Chromatophore-bearing Protozoa usually possess also a **stigma** (Fig. 31) or eye-spot. The stigma may occur in exceptional cases in colorless forms, as in *Khawkinea* according to Jahn. It is ordi-

narily situated in the anterior region and appears as a reddish or brownish red spot or rod, embedded in the cortical layer of the cytoplasm. The color of the stigma is due to the presence of droplets of haematochrome in a cytoplasmic network. The stigma is incapable of division and a new one is formed *de novo* at the time of cell division. In many species, the stigma possesses no accessory parts, but, according to Mast, the pigment mass in *Chlamy-*

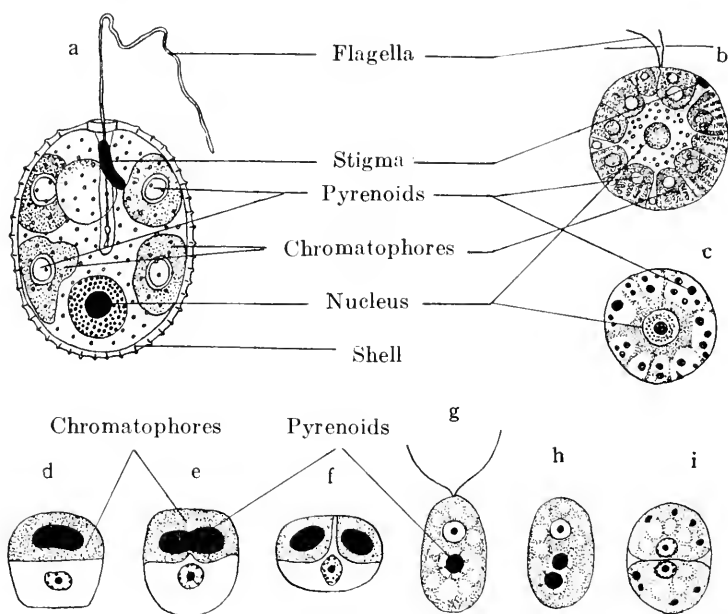


FIG. 31. a, *Trachelomonas hispida*, $\times 530$ (Doflein); b, c, living and stained reproductive cells of *Pleodorina illinoisensis*, $\times 1000$ (Merton); d-f, terminal cells of *Hydrurus foetidus*, showing division of chromatophore and pyrenoid (Geitler); g-i, *Chlamydomonas* sp., showing the division of pyrenoid (Geitler).

domonas, *Pandorina*, *Eudorina*, *Euglena*, *Trachelomonas*, etc., is in cup-form, the concavity being deeper in the colonial than in solitary forms. There is a colorless mass in the concavity, which appears to function as a lens. In certain dinoflagellates, there is an **ocellus** (Fig. 101, c, d, g, h) which is composed of amyloid lens and a dark pigment mass (melanosome) that is sometimes capable of amoeboid change of form. The stigma is, in general, regarded as an organella for the perception of light intensity. Mast considers

that the stigma in the Volvocidae is an organella which determines the direction of the movement.

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CHAPTER 4

Physiology

THE morphological consideration which has been given in the last chapter, is, though necessarily brief, indicative of the occurrence of various and often complex organellae in Protozoa. The physiological activity of the whole protozoan is the sum-total of all the functions which are carried on by numerous minute parts or organellae of the cell body, unlike the condition found in a metazoan. Indeed, as Calkins (1933) stated, "physiological problems (of Protozoa) for the most part begin where similar problems of the Metazoa leave off, namely the ultimate processes of the single cell. Here the functional activities have to do with the action and interaction of different substances which enter into the make-up of protoplasm and, for the most part, these are beyond our powers of analysis." A full discussion of various physiological problems pertaining to Protozoa is out of question in the present work and, therefore, a general consideration on protozoan physiology will suffice for our purpose.

Nutrition

The Protozoa obtain nourishment in manifold ways, which may be placed under three types: *holozoic*, *holophytic*, and *saprophytic*.

Holozoic (zootrophic, heterotrophic) nutrition. This is the method by which all higher animals obtain their nourishment; namely, the protozoan uses other animals or plants as sources of food. It involves the food-capture and ingestion, the digestion and assimilation, and rejection of indigestible portions.

The methods of food-capture vary among different forms. In the Sarcodina, the food organisms are captured and taken into the body at any point. The methods however vary. According to Rhumbler's oft-quoted observations, four methods of food-ingestion occur in amoebae (Fig. 32); namely, 1) by "import," in which the food is taken into the body upon contact, with very little movement on the part of the amoeba (*a*); by "circumfluence," in which the cytoplasm flows around the food organism as soon as it comes in contact with it on all sides and engulfs it (*b*); 3) by "cir-

cumvallation," in which the amoeba without contact with the food, forms pseudopodia which surround the food on all sides and ingest it (c); 4) by "invagination," in which the amoeba touches and adheres to the food, and the ectoplasm in contact with it is

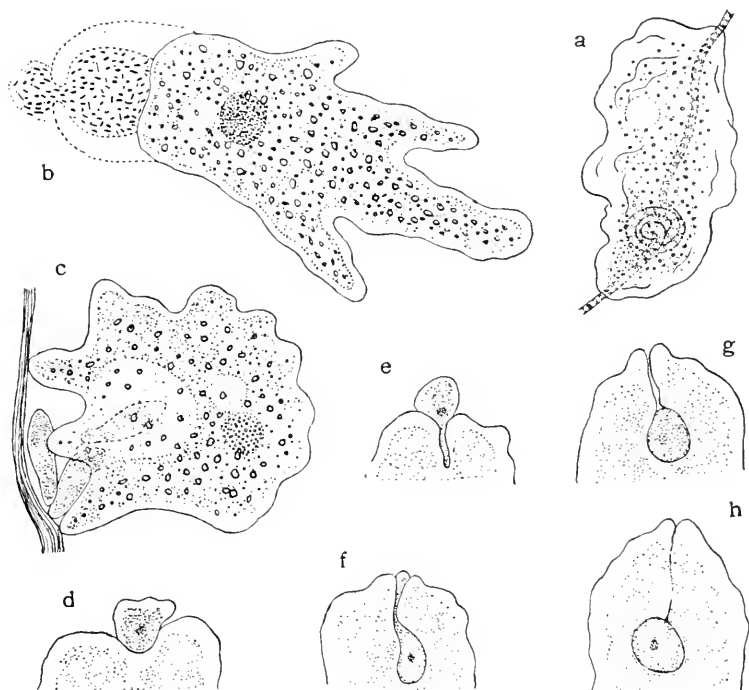


FIG. 32. Various ways by which amoebae capture food organisms. a, *Amoeba verrucosa* feeding on *Oscillatoria* by 'import' (Rhumbler); b, *A. proteus* feeding on bacterial glea by 'circumfluence'; c, on *Paramecium* by 'circumvallation' (Kepner and Whitlock); d-h, *A. verrucosa* ingesting a food particle by 'invagination' (Gross-Allermann).

invaginated into the endoplasm as a tube, the cytoplasmic membrane later liquefies and disappears (d-h). Jennings, Kepner, Schaeffer and others, have made studies with reference to the food-ingestion in amoebae.

In certain testaceans, such as *Gromia*, several rhizopodia cooperate in engulfing the prey and, in *Lieberkuhnia* (Fig. 33), Verworn noted ciliates are captured and digested in the rhizopodium.

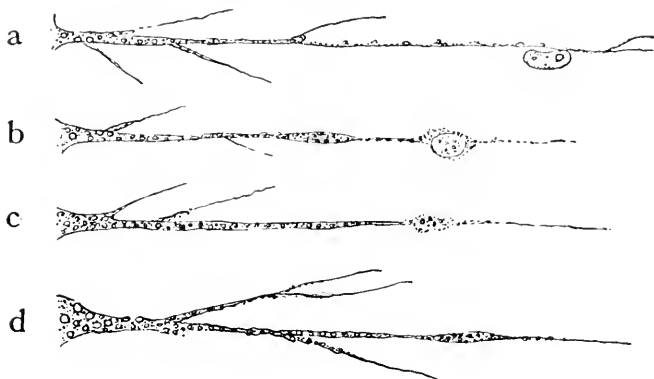


FIG. 33. A filopodium of *Lieberkuhnia*, capturing and digesting *Colpidium colpoda* (Verworn).

Similar observation was made by Schaudinn in the heliozoan *Camptonema* in which several axopodia anastomose to capture a prey (Fig. 163, *d*). In the holozoic Mastigophora, such as *Hypermastigina*, which do not possess cytostome, the food-ingestion is by pseudopodia also.

The food particles become attached to the pseudopodium and are held there on account of the viscid nature of the pseudopodium. The sudden immobility of active organisms upon coming in contact with pseudopodia of certain forms, such as *Actinophrys*, *Actinosphaerium*, *Gromia*, *Elphidium*, etc., suggests, however, probable discharge of poisonous substances. In the Suctoria which lack a cytostome, the tentacles serve as food-capturing organelles. The suctorial tentacle bears on its distal end a rounded knob which, when it comes in contact with an actively swimming ciliate, stops the latter immediately (*Parapodophrya typha*, Fig. 287, *a*). The prehensile tentacles of Ephelotidae are said to be similar in structure to the axopodia, in that each possesses a bundle of axial filaments around a cytoplasmic core (Roskin). These tentacles are capable of piercing through the body of a prey. In some suctorians, such as *Choanophrya* (Fig. 291, *a*), the tentacles are said to be tubular, and both solid and liquid food materials are sucked in through the cavity. The rapidity with which a tentacle of a suctorian stops a very actively swimming ciliate is attributed to a certain substance secreted by the tentacles which paralyzes the prey.

In the cytostome-bearing Mastigophora, the lashing of flagella will aid in bringing about the food-particles to the cytostome, where it is taken into the endoplasm. In the ciliates there are numerous types of cytostomes and associated organellae. But food-capturing seems to be in general of two kinds. When the cytostome is permanently open, the organism ingests food-particles which are small enough to pass the cytostome and cytopharynx, as in the case of *Paramecium*. Another type is one, such as noted in *Coleps*, *Didinium*, etc., where the ciliate attacks other organism and sucks in the body substance of the latter through the enlarged cytostome.

The ingested food-particles are always surrounded by a film of fluid which envelops the organism and the whole is known as the food vacuole (p. 77). The quantity of fluid taken in with the food varies greatly and, generally speaking, seems to be inversely proportional to the size, but proportional to the activity, of the food organisms. Food vacuoles composed entirely of surrounding liquid medium have occasionally been observed. Edwards (1925) observed ingestion of fluid-medium by an amoeba by forming food-cups under changed chemical composition. Brug (1928) reports seeing *Entamoeba histolytica* engulf liquid culture medium by formation of lip-like elevation of the ectoplasm and Kirby (1932) figures ingestion of the brine containing no visible organisms by the cytostome of *Rhopalophrya salina*. Mast and Doyle (1934) stated that if *Amoeba proteus*, *A. dubia*, *A. doleini*, or *A. radiosa* is placed in an albumin solution, a hypertonic balanced salt solution or a hypertonic solution of calcium gluconate, it rapidly decreases in volume, and forms numerous tubes filled with fluid, which disintegrate sooner or later and release their fluid content in the cytoplasm. At times 50 or more such tubes may be present, which indicate that the organism ingests considerable quantities of fluid in this way. The two authors consider that it is "a biological adaptation which serves to compensate for the rapid loss of water." The food vacuoles finally reach the endoplasm and in forms such as *Amoebina*, the vacuoles are carried about by the moving endoplasm. In the ciliates, the fluid endoplasm often shows a definite rotation movement. In *Paramecium*, the general direction is along one side up to the anterior end and down the other side, with a short cyclosis in the posterior half of the body. In *Carchesium*, according to Greenwood, the food-vacuoles pass

down to one end of the macronucleus and then move close to its concave surface to near the anterior end of the nucleus where defecation to the vestibule takes place (Fig. 34).

As stated above, in a number of species the food organisms are paralyzed or killed upon contact with pseudopodia, tentacles or exploded trichocysts. In numerous other cases, the captured or-

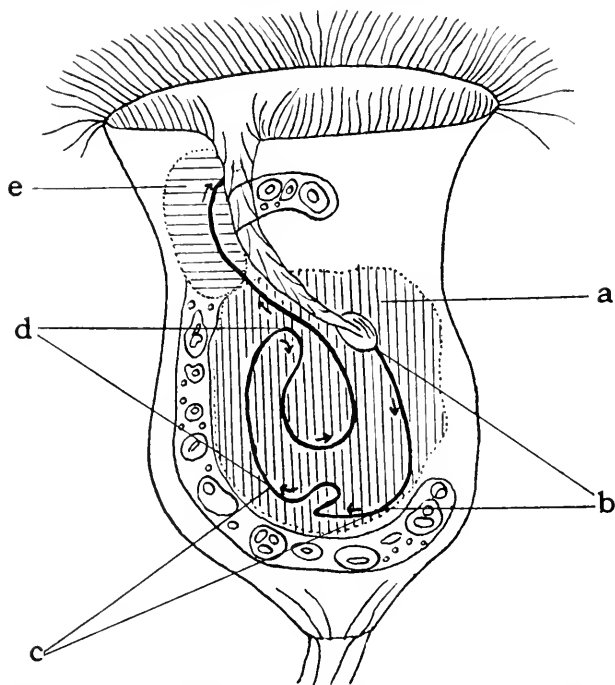


FIG. 34. Diagram showing the digestion within the food vacuoles in *Carchesium polypinum* (Greenwood). a, digestion area; b, region of little change; c, region of acid reaction; d, region of neutral reaction; e, defecation area.

ganism is taken into the food-vacuole alive, as will easily be noted by observing *Chilomonas* taken in by *Amoeba proteus* or actively moving bacteria ingested by *Paramecium*. But the prey ceases to move in a very short time. Apparently some substances are secreted into the food vacuole by the protoplasm of the organisms to stop the activity of the prey within the food vacuole. Engelmann (1878) demonstrated that the granules of blue litmus, when ingested by *Paramecium* or *Amoeba*, became red in a few minutes.

Brandt (1881) examined the staining reactions of amoebae by means of haematoxylin, and found that the watery vacuoles contained acid. Metschnikoff (1889) also showed that there appears an acid secretion around the ingested litmus grains in Mycetozoa. Greenwood and Saunders (1884) found in *Carchesium* that ingestion of food particles stimulated the cytoplasm to secrete a

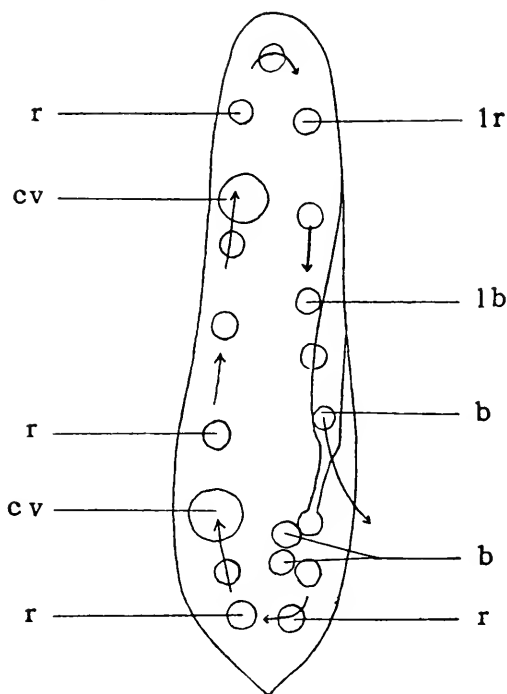


FIG. 35. Diagram showing changes in reactions in food-vacuoles of *Paramecium caudatum*, after ingesting litmus (Shapiro). b, blue; cv, contractile vacuole; lb, light blue; lr, light red; r, red.

mineral acid (Fig. 34). According to Nirenstein (1925), the food vacuole in *Paramecium* undergoes change in reaction which can be grouped in two periods. The first is acid reaction and the second alkaline reaction, in which albumin digestion takes place. On the other hand, Khainsky (1910) observed that the food vacuole of ciliates, such as *Paramecium*, is acid during the entire period of protein digestion, and becomes neutral to finally alkaline when the solution of the food substance is ended. Metchnikoff (1912)

found in the food vacuoles of *Paramecium*, besides acid-alkaline reaction change, that some vacuoles never show acid reaction and others occasionally show sustained acid reaction. According to Shapiro (1927), who observed reaction change of the food vacuoles in *Paramecium caudatum* (Fig. 35) by using phenol red, neutral red, Congo red, and litmus, when the organism is kept in a medium with pH 7, its food vacuoles are first alkaline (pH 7.6), soon reach a maximum acidity (pH 4.0), while still in the posterior half of the body. Later, the vacuoles show a decreased acidity, finally reaching pH 7.0 prior to excretion. In *Vorticella* sp. and *Stylonychia pustulata*, the range of pH observed in the food vacuoles was said to be 4.5–7.0 and 4.8–7.0 respectively. The food vacuoles of *Actinosphaerium*, according to Howland (1928), possess at the beginning pH 6.0–7.0 for 5 to 10 minutes, but this soon changes to acid (pH 4.3) in which digestion appears to be carried on. In older food vacuoles which are of less acid (pH 5.4–5.6), the digestion appears to be at an end.

Just exactly what processes take place in the food vacuole have been observed only in a few cases. Nirenstein noticed the appearance of numerous neutral red-stainable granules around the food vacuole which pass into the inside of the vacuole, and regarded them as carriers of a tryptic ferment, while Roskin and Levinsohn demonstrated the oxidase reaction in these granules. A number of enzymes have been reported in the Protozoa, some of which are mentioned on page 91.

These findings suffice to indicate that the digestion in Protozoa is carried on also by enzymes and its course appears to vary among different Protozoa. The albuminous substances are digested and decomposed into simpler compounds by enzymes and absorbed by the surrounding cytoplasm. The power to digest starch into soluble sugars is widely found among various Protozoa. It has been reported in Mycetozoa, Foraminifera, *Pelomyxa*, *Amoeba*, *Entamoeba*, *Ophryoscolecidae* and other ciliates by several investigators. In *Pelomyxa*, Stolc (1900) found that the so-called refractile bodies are intimately associated with the carbohydrate metabolism in that they are filled with glycogen which amount is proportionate to the food matter the organism obtains.

The members of *Vampyrella* (p. 291) are known to dissolve the cellulose wall of algae, especially *Spirogyra* in order to feed on

Protozoa	Enzymes	Observers
<i>Aethalium septicum</i>	Pepsin-like enzyme, dissolving albumins in acid medium	Krukenberg (1886)
<i>Pelomyxa palustris</i>	Pepsin-like and diastatic enzymes	Hartog and Dixon (1893)
Soil amoebae	"Amoebodiastase": trypsin-like, active in neutral or slightly alkaline medium, liquefies gelatin, coagulates albumin, inactive at 60°C.	Mouton (1902)
<i>Balantidium coli</i>	Diastatic enzyme	Glaessner (1908)
<i>Glaucoma pyriformis</i>	Proteolytic enzyme, capable of hydrolyzing casein	Lwoff (1932)
<i>Colpidium striatum</i>	Proteolytic enzyme, capable of hydrolyzing casein	Elliott (1933)
Poly- and Hypermastigina in wood roach	Cellulase; Cellobiase	Cleveland et al. (1934)

their contents. *Pelomyxa* (Stole), Foraminifera (Schaudinn), *Amoeba* (Rhumbler), *Hypermastigina*, *Polymastigina* (Cleveland), etc., have also been known for possessing the power of cellulose digestion. Many of the *Hypermastigina* and *Polymastigina* which lead symbiotic life in the intestine of the termite and the wood roach, as demonstrated by Cleveland and his coworkers, digest by enzymes the cellulose which the host insect ingests. The assimilation products produced by an enormous number of these flagellates are seemingly sufficient to support the protozoans as well as the host. The ciliate commensals inhabiting the stomach of ruminants also apparently digest the cellulose, since the fecal matter as a rule does not contain this substance. The digestion of fat by Protozoa had not been known, although oils and fat have been observed in numerous Protozoa, until Dawson and Belkin (1928) injected different oils into *Amoeba dubia* and found that from 1.4 to 8.3 per cent of the injected oil was digested.

The indigestible residue of the food is extruded from the body. The extrusion may take place at any point on the surface in many Sarcodina by a reverse process of ingestion of food. But in pelli-

ele-bearing forms, the defecation takes place either through the cytopyge located in the posterior region of the body or through an aperture to the vestibule (in *Carchesium*). Permanent cytopyge is lacking in some forms. In *Fabrea salina*, Kirby (1934) noticed that a large opening is formed at the posterior end, the contents of food vacuoles discharged, and the opening closes over. At first the margin of the body is left uneven, but soon the evenly rounded outline is restored. The same seems to be the case with *Spirostomum* (Fig. 36), *Blepharisma*, etc.

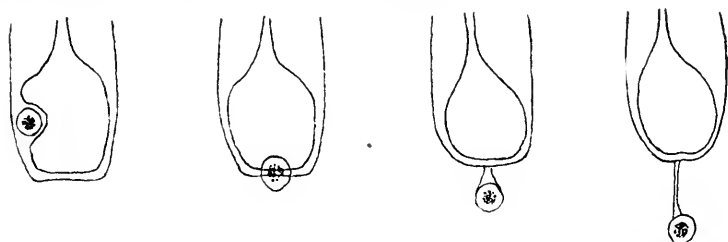


FIG. 36. Outline sketches showing the defecation process in *Spirostomum ambiguum* (Blättner).

Holophytic (autotrophic, phytotrophic) nutrition. This is the type of nutrition in which the Protozoa are able to decompose carbon dioxide by means of chlorophyll contained in chromatophores (p. 78) in the presence of the sunlight, liberating the oxygen and combining the carbon with other elements derived from water and inorganic salts. The pyrenoids (p. 79) are inseparably connected with the reserve carbohydrate formation in this nutrition. Aside from the Phytomastigina, chromatophores were definitely observed in *Cyclotrichium meunieri* (Fig. 230, o) by Powers. In a number of other cases, the organism itself is without chromatophores but is apparently not holozoic, because of the presence of chlorophyll-bearing organisms within it. For example, in the testacean *Paulinella* (Fig. 155, c) in which occur no food vacuoles, chromatophores of peculiar shape are always present. The latter appear to be a species of algae which holds a symbiotic relationship with the testacean, and perhaps it acts for the sarcodinan as the chromatophores of the Phytomastigina.

Saprozoic (saprophytic) nutrition. In this nutrition, the Protozoa obtain nourishment by diffusion through the body surface. This is accomplished without any special organellae. Perhaps the

only instance in which the saprozoic nutrition is accomplished through a special organella is the **pusules** (Figs. 101, 102) in marine dinoflagellates which, according to Kofoed and Swezy, appear to contain decomposed organic matter and aid the organisms in carrying on this process. The dissolved food matters are simpler compounds which have originated in animal or vegetable matter due to the decomposing activities of bacterial organisms. Numerous free-living Zoomastigina nourish themselves with this method. Recently a number of investigators found that saprozoic Protozoa could be cultivated in bacteria-free media of known compositions. For example, Pringsheim observed in *Polytoma uvella* (Fig. 91, *h*) that sodium acetate is needed from which the starch among others is produced, and carbohydrates have no direct bearing upon the nutrition, but fatty acids derived from them participate in the metabolism. Hall, Jahn, Loefer and others are following the same line of work which may lead to a better understanding of saprozoic nutrition as found in Protozoa.

The Protozoa which live within the body of another organism are able to nourish themselves by absorbing the digested or decomposed substances of the host and could be considered as saprozoic though **parasitic** has sometimes been used. Coelozoic Protozoa belong to this group, as for example, Protozoa, astomous ciliates, Trypanosomidae, etc. In the case of cytozoic or certain histozoic forms, such as Cnidosporidia, the host cytoplasm is apparently liquefied or hydrolyzed by enzymes (?) before being absorbed by the latter. The parasitic Protozoa, which actually feed on host tissue cells, such as *Entamoeba histolytica*, *Balantidium coli*, etc., or endocommensals, employ, of course, the holozoic nutrition.

Many Protozoa nourish themselves by more than one method at the same or different times, subject to a change in external conditions. This is sometimes referred to as **mixotrophic** nutrition (Pfeiffer). For example, *Euglena gracilis*, according to Zumstein (1889) and Lwoff (1932) loses its green coloration and becomes Astasia-like in the dark, or even in the light when the culture medium is very abundant in decomposed organic substances, which would indicate that this organism is capable of carrying on both holophytic and saprozoic nutrition. On the other hand *Chlorogonium euchlorum* and *C. elongatum* are said, according to Loefer (1934), to retain their green coloration after a year of cultivation

in total darkness, although the chromatophores appear somewhat modified.

The reserve food matter

The anabolic activities of Protozoa result in the growth and increase in volume of the organism, and also in the formation and storage of reserve food-substances which are deposited in the cytoplasm to be utilized later for growth or reproduction. The reserve food stuff is ordinarily glycogen or glycogenous substances, which seem to be present widely. Thus, in saprozoic Gregarinida, there occur in the cytoplasm numerous refractile bodies which stain brown to brownish-violet in Lugol's solution; are insoluble in cold water, alcohol, ether; become swollen and later dissolved in boiling water; and are reduced to a sugar by boiling in dilute sulphuric acid. This substance which composes the refractile bodies is called **paraglycogen** (Bütschli) or zooamylum. The abundant glycogen bodies of *Pelomyxa* have already been mentioned (p. 90). Rumjantzew and Wermel demonstrated glycogen in *Actinosphaerium*. In *Iodamoeba*, glycogen body is conspicuously present and is taken as a characteristic feature of the organism. The iodophile vacuole of the spores of *Myxobolidae* is a conspicuously well-defined vacuole containing glycogenous substance and is also considered as possessing a taxonomic value. In many ciliates, both free-living (*Paramecium*, *Glaucoma*, *Vorticella*, etc.) and endozoic (*Ophryoscolecidae*, *Nyctotherus*, *Balantidium*, etc.), glycogenous bodies are always present.

The anabolic products of the holophytic nutrition are starch, paramylon, oil and fats. The **paramylon** bodies are of various forms among different species, but appear to maintain a certain characteristic form within a species and can be used to a certain extent in taxonomic consideration. According to Heidt (1937), the paramylon of *Euglena sanguinea* (Fig. 37) is spirally coiled which confirms Bütschli's observation. The paramylon appears to be a polysaccharide which is insoluble in boiling water, but dissolves in concentrated sulphuric acid, potassium hydroxide, and slowly in formaldehyde. It does not stain with either iodine or chlor-zinc-iodide and when treated with a dilute potassium hydroxide, the paramylon bodies become enlarged and frequently exhibit a concentric stratification.

In the Chrysomonadina, the reserve food material is in the form of refractile bodies which are collectively called **leucosin**,

probably a carbohydrate. **Oils** occur in various Protozoa and when there is a sufficient number of oil producing forms in a body of water, the water may develop various odors. Whipple lists the following Protozoa, each of which if present in large numbers, may produce an offensive odor: *Cryptomonas* (candied violets), *Mallomonas* (aromatic, violets, fishy), *Synura* (ripe cucumber, muskmelon, bitter and spicy taste), *Uroglenopsis* (fishy, cod-liver oil-like), *Dinobryon* (fishy, like rockweed), *Chlamydomonas* (fishy, unpleasant or aromatic), *Eudorina* (faintly fishy), *Pandorina* (faintly fishy), *Volvox* (fishy), *Ceratium* (vile stench, rusty

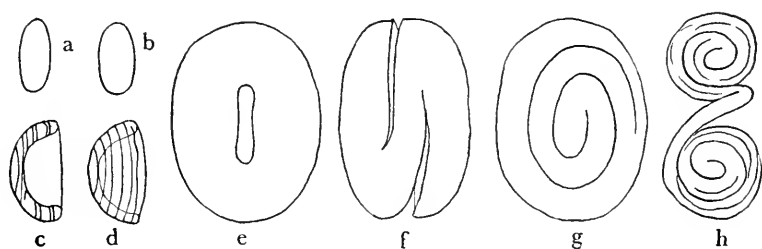


FIG. 37. a-d, two types of paramylon present in *Euglena gracilis* (Bütschli); e-h, paramylon of *E. sanguinea*, $\times 1100$ (Heidt). e, natural appearance; dried forms; h, strongly pressed bodies.

brown color), *Glenodinium* (fishy), *Peridinium* (fishy, like clamshells), and *Bursaria* (Irish moss, salt marsh, fishy).

Fats have also been detected in many Protozoa, such as Myxosporidia, Protociliata, certain Euciliata, Trypanosoma, etc. According to Panzer, the fat contents of *Eimeria gadi* was 3.55 per cent and Pratje reports that 12 per cent of the dry matter of *Noctiluca scintillans* appeared to be the fatty substance present in granular forms and which are said to give **phosphorescence** upon mechanical or chemical stimulation. A number of other dinoflagellates, such as *Peridinium*, *Ceratium*, *Gonyaulax*, *Gymnodinium*, etc., also emit phosphorescence. In other forms the fats may be hydrostatic in function, as is the case with a number of pelagic Radiolaria.

Another reserve food-stuff which occurs widely in Protozoa, excepting Ciliophora, is the so-called **volutin** or metachromatic granules. It is apparently equally widely present in Protophyta. In fact it was first discovered in the protophytan *Spirillum volutans*. Meyer coined the name and held it to be made up of a nu-

eleic acid. It stains deeply with nuclear dyes. Reichenow (1909) demonstrated that if *Haematococcus pluvialis* (Fig. 38) was cultivated in phosphorus-free medium the volutin is quickly used up and does not reappear. If however, the organisms are cultivated in a medium rich in phosphorus, the volutin increases greatly in volume and, as the culture becomes old, it gradually breaks down. In *Polytomella agilis* (Fig. 92, c, d), Doffein showed that an addition of sodium phosphate resulted in an increase of volutin. Reichenow, Schumacher, and others, hold that the volutin appears

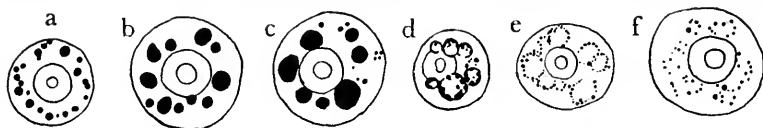


FIG. 38. *Haematococcus pluvialis*, showing the development of volutin in the medium rich in phosphorus and its disintegration in exhausted medium, $\times 570$ (Reichenow). a, second day; b, third day; c, fourth day; d, e, sixth day; f, eighth day.

to be a free nucleic acid, and is a special reserve food material for the nuclear substance. Recently Sassuchin (1935) studied the volutin in *Spirillum volutans* and *Sarcina flava* and found that the volutin appears during the period of strong growth, nourishment and multiplication, disappears in unfavorable condition of nourishment and gives a series of characteristic carbohydrate reactions. Sassuchin considers that the volutin is not related to the nucleus, but is reserve food material of the cell, which is composed of glykoproteid.

Respiration

In order to carry on various vital activities, the Protozoa, like all other organisms, must transform the potential energy stored in highly complex chemical compounds present in the cytoplasm, into various forms of active energy by oxidation. The oxygen involved in this process appears to be brought into contact with the substances in two ways in Protozoa. The great majority of free-living, epizoid and certain endozoic forms absorb free molecular oxygen from the surrounding media. The absorption of oxygen appears to be carried on by the permeable body surface, since there is no special organella for this purpose. The polysaprobic Protozoa are known to live in water containing no free oxygen.

For example, Noland (1927) observed *Metopus es* in a pool, 6 feet in diameter and 18 inches deep, filled with dead leaves which gave a strong odor of hydrogen sulphide. The water in it showed pH 7.2 at 14°C., and contained no dissolved oxygen, 14.9 c.c. per liter of free carbon dioxide, and 78.7 c.c. per liter of fixed carbon dioxide. It is considered that endozoic Protozoa of metazoan digestive systems live also in a medium containing no dissolved oxygen. All these forms appear to possess capacity of splitting complex oxygen-bearing substances present in the body to produce necessary oxygen. The liberation of energy is accompanied by production of water and carbon dioxide.

Several investigators studied the influence of abundance or lack of oxygen upon different Protozoa. For example, Pütter demonstrated that several ciliates reacted differently when subjected to anaerobic condition, some perishing rapidly, others living for a considerable length of time. Death is said by Löhner to be brought about by a volume-increase due to accumulation of the waste products. When first starved for a few days and then placed in anaerobic environment, *Paramecium* and *Colpidium* died much more rapidly than unstarved individuals. Pütter, therefore, supposed that the difference in longevity of aerobic Protozoa in anaerobic conditions was correlated with that of the amount of reserve food material such as protein, glycogen and paraglycogen present in the body. Noting *Paramecium* is less affected by anaerobic conditions than *Spirostomum* in a small amount of water, Pütter maintained that the smaller the size of Protozoa and the more elaborate the contractile vacuole system, they suffer the less lack of oxygen in the water, since the removal of catabolic waste depends upon these factors.

The variety of habitats and results of artificial cultivations of various Protozoa clearly indicate that the oxygen requirements vary a great deal among different forms. Attempts were made in recent years to determine the oxygen requirement of Protozoa. The results of the observations are not always convincing. The oxygen consumption of *Paramecium* is said, according to Lund (1918) and Amberson (1928), to be fairly constant over a wide range of oxygen concentration. Specht (1934) considers the measurements of the oxygen consumption and carbon dioxide production in *Spirostomum ambiguum* vary because of the presence of a base produced by the organism. Soule (1925) observed in the cul-

tural tubes of *Trypanosoma lewisi* and *Leishmania tropica*, the oxygen contained in about 100 c.c. of air of the test tube is used up in about 12 and 6 days respectively. A single *Paramecium caudatum* is said to consume in one hour at 21°C. from 0.0052 c.c. (Kalmus) to 0.00049 c.c. (Howland and Bernstein) of oxygen. *Amoeba proteus*, according to Hulpieu (1930), succumbs slowly when the amount of oxygen in water is less than 0.005 per cent and also in excess, which latter confirms Pütter's observation of *Spirostomum*. The *Hypermastigina* of the termite are killed, according to Cleveland, when the host animals are kept in an excess of oxygen. Jahn (1935) found that *Chilomonas paramecium* in bacteria-free cultures in heavily buffered peptone-phosphate media at pH 6.0 required for rapid growth carbon dioxide which apparently brings about a favorable intracellular hydrogen-ion concentration.

Excretion and secretion

The catabolic waste material composed of water, carbon dioxide, urea and other nitrogenous compounds, all of which are soluble, pass out of the body by diffusion through the surface or by means of the contractile vacuole (p. 73). The protoplasm of the Protozoa is generally considered to possess a molecular make-up which appears to be similar among those living in various habitats. In the freshwater Protozoa, the water diffuses through the body surface and so increases the water contents of the body protoplasm as to interfere with its normal function. The contractile vacuole, which is invariably present in all freshwater forms, is the means of getting rid of this excess water from the body. On the other hand, marine or endozoic Protozoa live in isotonic media and there is no excess of water entering the body, hence the contractile vacuoles are not found in them. Just exactly why all ciliates and suctorians possess the contractile vacuole regardless of habitat, has not been explained. There are accumulating evidences to indicate that the pellicle of the ciliate is impermeable to water and salts, and that the water enters the ciliate body through the cytostome and cytopharynx only. Frisch (1937) observed recently such is the case in *Paramecium multimicronucleata*. If this is true in all ciliates, it is quite easy to understand the universal occurrence of the contractile vacuole in the cytostome-bearing ciliates. However, it does not explain all cases, as a number of astomous ciliates with a definite pellicle possess contractile vacuoles (p. 488).

That the elimination of excess amount of water from the body is one of the functions of the contractile vacuole appears to be beyond doubt judging from the observations of Zuelzer (1907), Finley (1930) and others, on *Amoeba verrucosa* which lost gradually its contractile vacuole as sodium chloride was added to the water, losing the organella completely in the seawater concentration. Herf (1922) studied the pulsation of the contractile vacuoles of *Paramecium caudatum* in fresh water as well as various salt concentrations, and obtained the following measurements:

Per cent NaCl in water	0	0.25	0.5	0.75	1.00
Contraction period in second	6.2	9.3	18.4	24.8	163.0
Excretion per hour in body volumes	4.8	2.82	1.38	1.08	0.16

The contractile vacuole also serves to remove from the body part of soluble catabolic wastes, judged by numerous observations. Weatherby (1929) showed that the contractile vacuoles of *Paramecium* and *Spirostomum* contain urea, and that of *Didinium* contains ammonia and occasionally trace of uric acid. The number of the contractile vacuoles present in a given species as in various species of *Paramecium*, is not always constant. Nor is its size constant. According to Taylor (1920) the average size of the contractile vacuole of *Euplotes patella* is 29μ at maximum diastole, but may become $45\text{--}50\mu$ in diameter upon disturbance or after incision. The rate of pulsation is subject to changes with temperature, physiological state of the organism, amount of food substances present in the water, etc. For example, Rossbach observed in the three ciliates mentioned below that the pulsation of the contractile vacuole increased first rapidly and then more slowly with the rise of the temperature of the water:

	Time in seconds between two systoles at different temperature (C.)					
	5°	10°	15°	20°	25°	30°
<i>Euplotes charon</i>	61	48	31	28	22	23
<i>Stylonychia pustulata</i>	18	14	10-11	6-8	5-6	4
<i>Chilodonella cucullulus</i>	9	7	5	4	4	—

Aside from the soluble forms, there often occur in the protozoan body insoluble catabolic products in the forms of **crystals** and **granules** of various kinds. Schewiakoff (1893) first noticed that *Paramecium* often contains crystals (Fig. 39) composed of calcium

phosphate, which disappeared completely in 1-2 days when the organisms were starved, and reappeared when food was given. Schewiakoff did not see the extrusion of these crystals, but considered that these crystals were first dissolved and excreted by the contractile vacuoles, as they were seen collected around the vacuoles. In *Amoeba proteus*, Schubotz (1905) noted that the crystals were of similar chemical composition and of usually bipyramidal or rhombic form, and that they measure about $2-5\mu$ in length and doubly refractile. Schaeffer (1920) observed calcium phosphate crystals in three species of *Amoeba* and was inclined to think that the form and dimensions of these crystals were

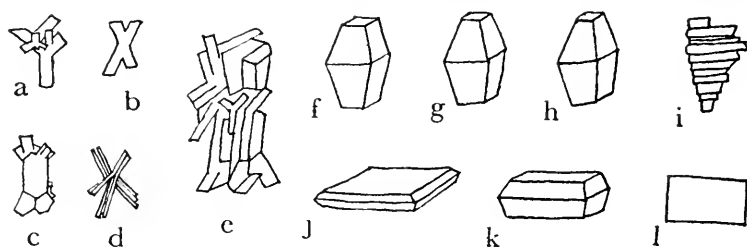


FIG. 39. Examples of crystals present in Protozoa. a-e, in *Paramecium caudatum* (Schewiakoff), (a-d, $\times 1000$, e, $\times 2600$); f, in *Amoeba proteus*; g, in *A. discoides*; h, in *A. dubia* (Schaeffer).

characteristic of each species. Thus in *Amoeba proteus*, they are truncate bipyramids, rarely flat plates, up to 4.5μ long; in *A. discoides*, abundant, truncate bipyramids, up to 2.5μ long; and in *A. dubia*, variously shaped (4 kinds) few, but large, up to 10μ , 12μ , 30μ long (Fig. 39).

Howland detected uric acid in *Paramecium caudatum* and *Amoeba verrucosa*. Luce and Pohl (1935) noticed that at certain times amoebae in culture are clear and contain relatively a few crystals but, as the culture grows older and the water becomes more neutral, the crystals become abundant and the organisms become opaque to transmitted light. These crystals are tubular and six-sided, and vary in length from 0.5 to 3.5μ . They considered the crystals were composed of calcium chlorphosphate. Mast and Doyle (1935), on the other hand, noted in *Amoeba proteus* two kinds of crystals, plate-like and bipyramidal, which vary in size up to 7μ in length and which are suspended in alkaline fluid to viscous vacuoles. These two authors believe that the plate-like

crystals are probably leucine, while the bipyramidal crystals consist of a magnesium salt of a substituted glycine. Other crystals are said to be composed of urate, carbonate, oxalate, etc.

Another catabolic product is the **melanin** grains which occur in many haemosporidians and which appear to be composed of a derivative of the haemoglobin of the infected erythrocyte. In certain Radiolaria, there occurs a brownish amorphous mass which is considered as catabolic waste material and, in Foraminifera, the cytoplasm is frequently loaded with masses of brown granules which appear also to be catabolic waste and are extruded from body periodically.

While intracellular secretions are usually difficult to recognize, because the majority remain in fluid form except those which produce endoskeletal structures occurring in Heliozoa, Radiolaria, certain parasitic ciliates, etc., the extracellular secretions are easily recognizable as loricae, shells, envelopes, stalks, collars, mucous substance, pigments which give the body a characteristic coloration (p. 37), etc. Furthermore, many Protozoa secrete, as was stated before, certain substances through the pseudopodia, tentacles or trichocysts which possess paralyzing effect upon the preys.

Movements

The Protozoa move about by means of the *pseudopodia*, *flagella*, or *cilia*, which may be combined with internal contractile organellae.

Movement by pseudopodia. The amoeboid movements have long been studied by numerous observers. The first attempt to explain the movement was by Berthold (1886), who held that the difference in the surface tension was the cause of amoeboid movements, which view was supported by the observations and experiments of Bütschli (1894) and Rhumbler (1898). According to this view, when an amoeba forms a pseudopodium, there probably occurs a diminution of the surface tension of the cytoplasm at that point, due to certain internal changes which are continuously going on within the body and possibly to external causes, and the internal pressure of the cytoplasm will then cause the streaming of the cytoplasm. This results in the formation of a pseudopodium which becomes attached to the substratum and an increase in tension of the plasma-membrane draws up the posterior

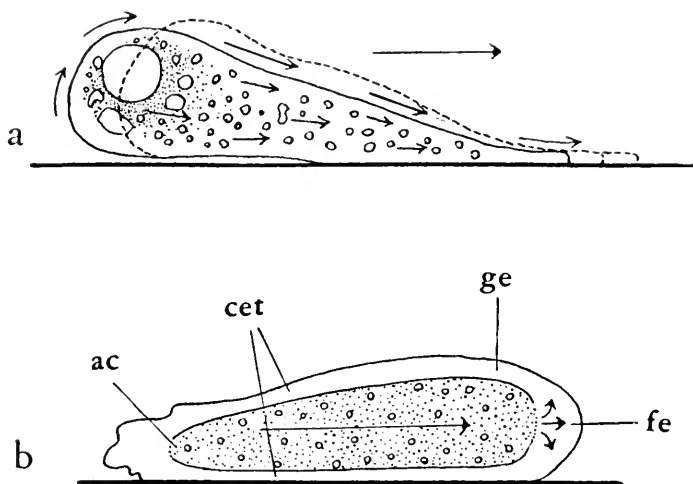


FIG. 40. a, diagram showing the movement of *Amoeba verrucosa* in side view (Jennings); b, a marine limax-amoeba in locomotion (Pantin from Reichenow). ac, area of conversion; cet, contracting ectoplasmic tube; fe, fluid ectoplasm; ge, gelated ectoplasm.

end of the amoeba, thus bringing about the movement of the whole body.

Jennings (1904) found that the movement of *Amoeba verrucosa* (Fig. 40, a) could not be explained by the surface tension theory, since he observed "in an advancing amoeba substance flows forward on the upper surface, rolls over at the anterior edge, coming in contact with the substratum, then remains quiet until the body of the amoeba has passed over it. It then moves upward at the posterior end, and forward again on the upper surface, continuing in rotation as long as the amoeba continues to progress." Thus *Amoeba verrucosa* may be compared with an elastic sac filled with fluid. Dellinger (1906) studied the movement of *Amoeba proteus*, *A. verrucosa* and *Diffugia spiralis*. Studying in side view, he found that the amoeba (Fig. 41) extends a pseudopod, "swings it about, brings it into the line of advance, and attached it" to the substratum and that there is then a concentration of the substance back of this point and a flow of the substance toward the anterior end. Dellinger held thus that "the movements of amoebae are due to the presence of a contractile substance," which was said to be located in the endoplasm as a coarse reticulum.

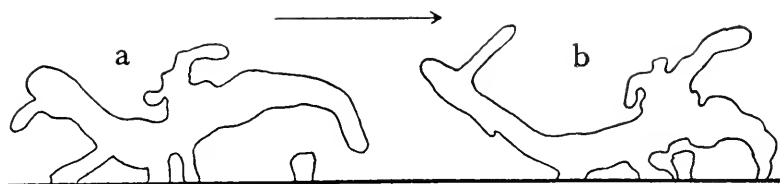


FIG. 41. Outline sketches of photomicrographs of *Amoeba proteus* during locomotion, as viewed from side (Dellinger).

In the face of advancement of our knowledge on the nature of protoplasm, Rhumbler realized the difficulties of the surface tension theory and later suggested that the conversion of the ectoplasm to endoplasm and vice versa were the cause of the cytoplasmic movements, which was much extended by Hyman (1917). Hyman considered that: 1) a gradient in susceptibility to potassium cyanide exists in each pseudopodium, being the greatest at the distal end, and the most recent pseudopodium, the most susceptible; 2) the susceptibility gradient (or metabolic gradient arises in the amoebae before the pseudopodium appears and hence the metabolic change which produces increased susceptibility, is the primary cause of pseudopodium formation; and 3) since the surface is in a state of gelation, amoeboid movement must be due to alterations of the colloidal state. Solation, which is brought about by the metabolic change, is regarded as the cause of the extension of a pseudopodium, and gelation of the withdrawal of pseudopodia and of active contraction. Schaeffer (1920) mentions the importance of the surface layer which is a true surface tension film, the ectoplasm, and the streaming of endoplasm in the amoeboid movement.

Pantin (1923) studied a marine limax-type amoeba (Fig. 40, b) and came to recognize acid secretion and absorption of water at the place where the pseudopodium was formed. This results in swelling of the cytoplasm and the pseudopodium is formed. Because of the acidity, the surface tension increases and to lower or reduce this, concentration of substances in the "wall" of the pseudopodium follows. This leads to the formation of a gelatinous ectoplasmic tube which, as the pseudopodium, extends moves toward the posterior region where the acid condition is lost, gives up water and contracts, finally becoming transformed into endoplasm near the posterior end. The contraction of

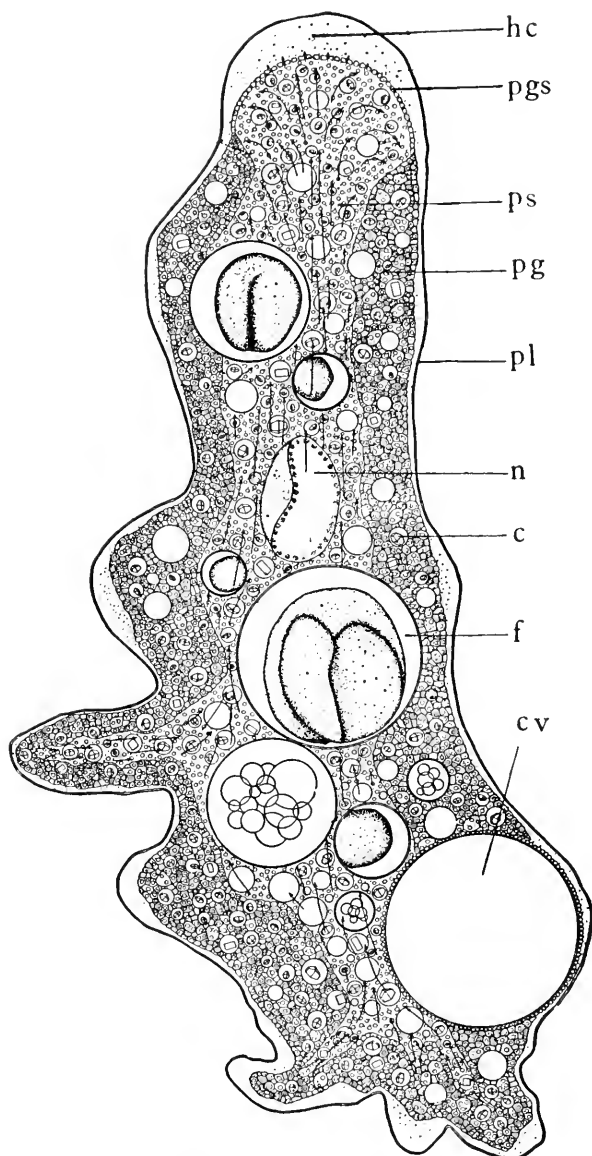


FIG. 42. Diagram of *Amoeba proteus*, showing the solation and gelation of the cytoplasm during amoeboid movement (Mast). c, crystal; cv, contractile vacuole; f, food vacuole; hc, hyaline cap; n, nucleus; pg, plasmagel; pgs, plasmagel sheet; pl, plasmalemma; ps, plasmasol.

the ectoplasmic tube forces the endoplasmic streaming to the front. This observation is in agreement with that of Mast (1923, 1926, 1931) who after a series of carefully conducted observations on *Amoeba proteus* came to hold that the amoeboid movement is brought about by "four primary processes; namely, attachment to the substratum, gelation of plasmasol at the anterior end, solation of plasmagel at the posterior end and the contraction of the plasmagel at the posterior end" (Fig. 42). As to how these processes work, Mast states: "The gelation of the plasmasol at the anterior

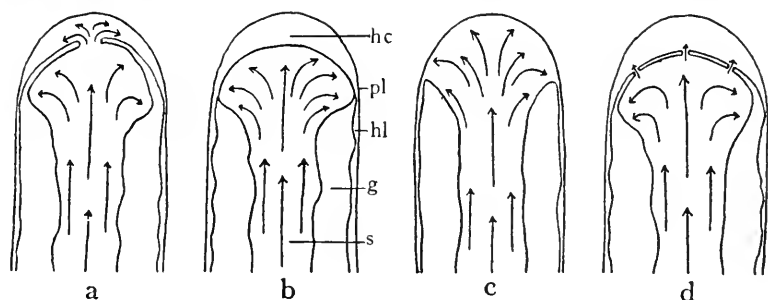


FIG. 43. Diagrams of varied cytoplasmic movements at the tip of a pseudopodium in *Amoeba proteus* (Mast). g, plasmagel; hc, hyaline cap; hl, hyaline layer; pl, plasmalemma; s, plasmasol.

end extends ordinarily the plasmagel tube forward as rapidly as it is broken down at the posterior end by solation and the contraction of the plasmagel tube at the posterior end drives the plasmasol forward. The plasmagel tube is sometimes open at the anterior end and the plasmasol extends forward and comes in contact with the plasmalemma at this end (Fig. 43, *a*), but at other times it is closed by a thin sheet of gel which prevents the plasmasol from reaching the anterior end (*b*). This gel sheet at times persists intact for considerable periods, being built up by gelation as rapidly as it is broken down by stretching, owing to the pressure of the plasmagel against it. Usually it breaks periodically at various places. Sometimes the breaks are small and only a few granules of plasmasol pass through and these gelate immediately and close the openings (*d*). At other times the breaks are large and plasmasol streams through, filling the hyaline cap (*c*), after which the sol adjoining the plasmalemma gelates forming a new gel sheet. An amoeba is a turgid system, and the plasmagel is under continuous tension. The plasmagel is elastic and, consequently, is

pushed out at the region where its elasticity is weakest and this results in pseudopodial formation. When an amoeba is elongated and undergoing movement, the elastic strength of the plasmagel is the highest at its sides, lowest at the anterior end and intermediate at the posterior end, which results in continuity of the elongated form and in extension of the anterior end. If pressure is brought against the anterior end, the direction of streaming of plasmasol is immediately reversed, and a new hyaline cap is formed at the posterior end which is thus changed into a new anterior end."

Flagellar movement. The flagellar movement is only in a few instances observable as in *Peranema*, but in most cases it is very difficult to observe in life. Since there is difference in the number, location, size, and probably structure (p. 45) of flagella occurring in Protozoa, it is supposed that there are varieties of flagellar movements. The first explanation was advanced by Bütschli, who observed that the flagellum undergoes a series of lateral movements and, in so doing, a pressure is exerted on the water at right angles to its surface. This pressure can be resolved into two forces: one directed parallel, and the other at right angles, to the main body axis. The former will drive the organism forward, while the latter will tend to rotate the animal on its own axis.

Gray (1928), who gave an excellent account of the movement of flagella, points out that "in order to produce propulsion there must be a force which is always applied to the water in the same direction and which is independent of the phase of lateral movement. There can be little doubt that this condition is satisfied in flagellated organisms not because each particle of the flagellum is moving laterally to and fro but by the transmission of the waves from one end of the flagellum to the other, and because the direction of the transmission is always the same. A stationary wave, as apparently contemplated by Bütschli, could not effect propulsion since the forces acting on the water are equal and opposite during the two phases of the movement. If however the waves are being transmitted in one direction only, definite propulsive forces are present which always act in a direction opposite to that of the waves."

Because of the nature of the flagellar movement, the actual process has often not been observed. Verworn observed long ago that in *Peranema trichophorum* the undulation of the distal por-

tion of flagellum is accomplished by a slow forward movement, while undulation along the entire length by a rapid forward movement. Recently Krijgsman (1925) studied *Monas* sp. (Fig. 44) which he found in soil cultures, under the darkfield microscope and stated: 1) when the organism moves forward with the maximum speed, the flagellum starting from *c1*, with the wave beginning at the base, stretches back (*c 1-6*), and then waves back (*d, e*), which brings about the forward movement. Another type is

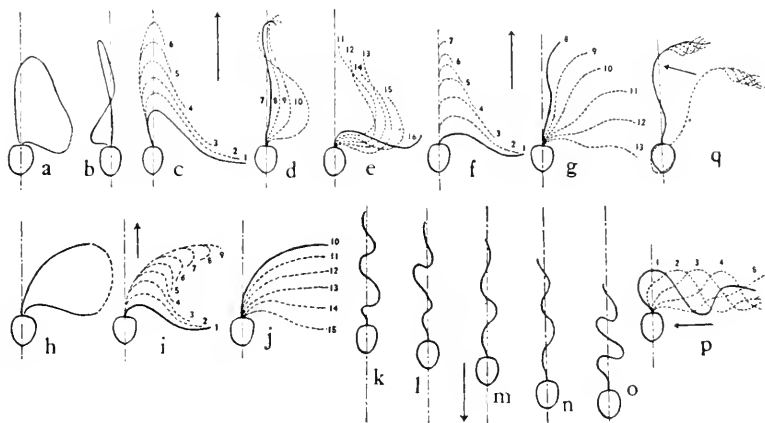


FIG. 44. Diagrams illustrating flagellar movements of *Monas* sp. (Krijgsman). a-g, rapid forward movement (a, b, optical image of the movement in front and side view; c, preparatory and d, e, effective stroke; f, preparatory and g, effective stroke); h-j, moderate forward movement (h, optical image; i, preparatory and j, effective stroke); k-o, undulatory movement of the flagellum in backward movement; p, lateral movement; q, turning movement.

one in which the flagellum bends back beginning at its base (f) until it coincides with the body axis, and in its effective stroke waves back as a more or less rigid structure (g); 2) when the organism moves forward with moderate speed, the tip of the flagellum passes through 45° or less (h-j); 3) when the animal moves backward, the flagellum undergoes undulation which begins at its base (k-o); 4) when the animal moves to one side, the flagellum becomes bent at right angles to the body and undulation passes along it from its base to tip (p); and 5) when the organism undergoes a slight lateral movement, the distal end of the flagellum only undulates (q).

Ciliary movement. The cilia are the locomotor organella present permanently in the ciliates and vary in size and distribution among different species. Just as flagellates show various types of movements, so do the ciliates. Individual cilium on a progressing ciliate bends throughout its length and strike the water so that the organism tends to move in a direction opposite to that of the effective beat, while the water moves in the direction of the beat (Fig. 45, *a-d*). In the *Protociliata* and the majority of *holotrichous* and *heterotrichous* ciliates, the cilia are arranged in longi-

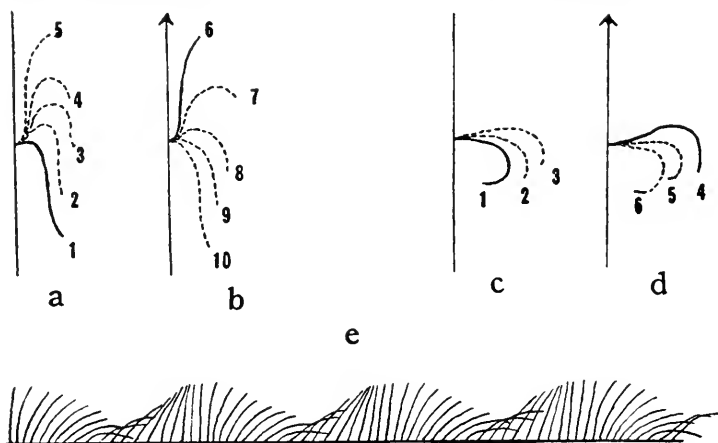


FIG. 45. Diagrams illustrating ciliary movements (Verworn). *a-d*, movement of a marginal cilium of *Urostyla grandis* (*a*, preparatory and *b*, effective stroke, resulting in rapid movement; *c*, preparatory, and *d*, effective stroke, bringing about moderate speed); *e*, metachronous movements of cilia in a longitudinal row.

tudinal, or oblique rows and it is clearly noticeable that the cilia are not beating in the same phase, although they are moving at the same rate. A cilium (Fig. 45, *e*) in a single row is slightly in advance of the cilium behind it and slightly behind the one just in front of it, thus the cilia on the same longitudinal row beat metachronously. On the other hand, the cilia on the same transverse row beat synchronously, the condition clearly being recognizable on *Opalina* among others, which is much like the waves passing over a wheat field on a windy day. The organized movements of cilia, cirri, membranellae and undulating membranes are probably controlled by the neuromotor system (p. 55) which

appears to be conductile as judged by the results of micro-dissection experiments of Taylor (p. 56).

The Protozoa which possess myonemes are able to move by contraction of the body or of stalk, and others combine this with the secretion of mucous substance as was found in *Haemogregarina* and *Gregarinida*.

Irritability

Under natural conditions, the Protozoa do not behave always in the same manner, because several stimuli act upon them usually in combination and predominating stimulus or stimuli vary under different circumstances. Many investigators have, up to the present time, studied the reactions of various Protozoa to external stimulations, full discussion of which is beyond the scope of the present work. Here one or two examples in connection with the reactions to each of the various stimuli will only be mentioned. Of various responses expressed by a protozoan against a stimulus, movement is the most clearly recognizable one and, therefore, free-swimming forms, particularly ciliates, have been the favorite objects of study. We consider the reaction to a stimulus in protozoans as the movement response, and this appears in one of the two directions: namely, toward, or away from, the source of the stimulus. Here we speak of positive or negative reaction. In forms such as *Amoeba*, the external stimulation is first received by the body surface and then by the whole protoplasmic body. In flagellated or ciliated Protozoa, these processes act in part sensory, in fact in a number of ciliates are found non-vibratile cilia which appear to be sensory in function. In a comparatively small number of forms, there are sensory organellae such as stigma (p. 79), ocellus (p. 80), statocysts (p. 77), concretion vacuoles (p. 77), etc.

In general, the reaction of a protozoan to any external stimulus depends upon its intensity so that a certain chemical substance may bring about entirely opposite reactions on the part of the protozoans in different concentrations and, even under identical conditions, different individuals of a given species may react differently.

Reaction to mechanical stimuli. One of the most common stimuli a protozoan would encounter in the natural habitat is that which comes from contact with a solid object. When an amoeba which Jennings observed, came in contact with the end

of a dead algal filament at the middle of its anterior surface (Fig. 46, *a*), the amoeboid movements proceeded on both sides of the filament (*b*), but soon motion ceased on one side, while it continued on the other, and the organism avoided the obstacle by reversing a part of the current and flowing in another direction (*c*). When an amoeba is stimulated mechanically by the tip of a glass rod (*d*), it turns away from the side touched, by changing endoplasmic streaming and forming new pseudopodia (*e*). Positive re-

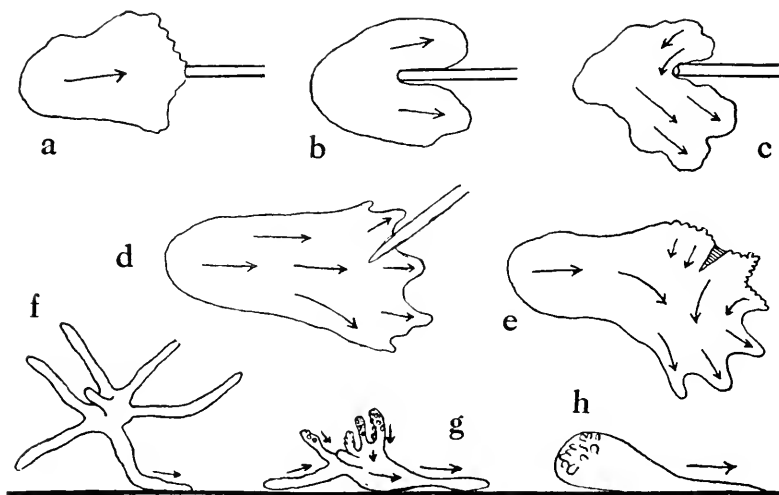


FIG. 46. Reactions of amoebae to mechanical stimuli (Jennings). *a*–*c*, an amoeba avoiding an obstacle; *d*, *e*, negative reaction to mechanical stimulation; *f*–*h*, positive reaction of a floating amoeba.

actions are also often noted, when a suspended amoeba (*f*) comes in contact with a solid surface with the tip of a pseudopodium, the latter adheres to it by spreading out (*g*). Streaming of the cytoplasm follows and it becomes a creeping form (*h*). Positive reactions toward solid bodies account of course for the ingestion of food particles.

In *Paramecium*, according to Jennings, the anterior end is more sensitive than any other parts, and while swimming, if it comes in contact with a solid object, the response may be either negative or positive. In the former case, avoiding movement (Fig. 47, *c*) follows and in the latter case, the organism rests with its anterior

end or the whole side in direct contact with the object, in which position it ingests food particles through the cytostome.

Reaction to gravity. The reaction to gravity varies among different Protozoa, according to body organization, locomotor organellae, etc. Amoebae, Testacea and others which are usually found attached to the bottom of the container, react as a rule positively toward gravity, while others manifest negative reac-

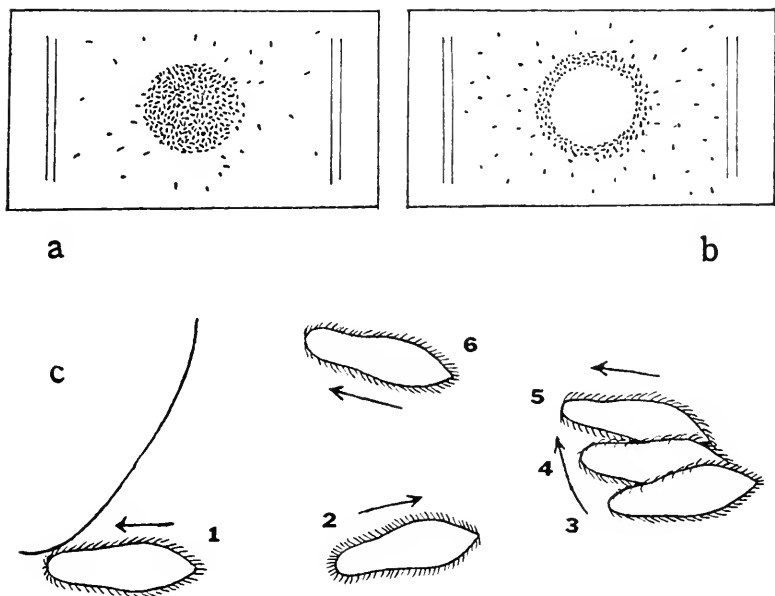


FIG. 47. Reactions of *Paramecium* (Jennings). a, collecting in a drop of 0.02% acetic acid; b, ring-formation around a drop of a stronger solution of the acid; c, avoiding reaction.

tion as in the case of *Paramecium* (Jensen; Jennings), which explains in part why *Paramecium* in a culture jar are found just below the surface film en masse, although, according to Dembowski (1929) the vertical movement of *Paramecium caudatum* is influenced by various factors.

Reaction to current. Free-swimming Protozoa appear to move or orientate themselves against the current of water. In the case of *Paramecium*, Jennings observed the majority place themselves in line with the current, with anterior end upstream. The mycetozoan is said to exhibit also a well-marked positive reaction.

Reaction to chemical stimuli. When methylgreen, methylene blue, or sodium chloride is brought in contact with an advancing amoeba, the latter organism reacts negatively (Jennings). Jennings further observed various reactions of *Paramecium* against chemical stimulation. This ciliate shows positive reaction to weak solutions of many acids and negative reactions above certain concentrations. For example, *Paramecium* enters and stays within the area of a drop of 0.02 per cent acetic acid introduced to the preparation (Fig. 47, *a*); and if stronger acid is used, the organisms collect about its periphery where the acid is diluted by the surrounding water (Fig. 47, *b*). The reaction to chemical stimuli is probably of the greatest importance for the existence of Protozoa, since it leads them to proper food substances, the ingestion of which is the foundation of metabolic activities. In the case of parasitic Protozoa, possibly the reaction to chemical stimuli results in their finding specific host animals and their distribution in different organs and tissues within the host body.

Reaction to light stimuli. Most Protozoa seem to be indifferent to the ordinary light, but when the light intensity is suddenly increased, there is usually a negative reaction. Verworn saw the direction of movements of an amoeba reversed when its anterior end was given a sudden illumination; Rhumbler observed that an amoeba, which was in the act of feeding, stopped feeding when it was subjected to strong light. According to Mast, *Amoeba proteus* ceases to move when suddenly strongly illuminated, but continues to move if the increase in intensity is gradual and if the illumination remains constant, the amoeba begins to move. According to Jennings, *Stentor coeruleus* reacts negatively against light.

The positive reaction to light is most clearly shown in stigma-bearing Mastigophora, as is well demonstrated by a jar containing *Euglena*, *Phacus*, etc., in which the organisms collect at the place where the strongest light reaches. If the light is excluded completely, the organisms become scattered throughout the container, inactive and sometimes encysted, although the mixotrophic forms would continue activities by saprozoic methods. The positive reaction to light by chromatophore-bearing forms enables them to find places in the water where photosynthesis can be carried on to the maximum degree.

All Protozoa seem to be more sensitive to ultraviolet rays. In-

man found that amoebae show a greater reaction to the rays and Hertel observed that *Paramecium* which were indifferent to an ordinary light, showed an immediate response (negative reaction) to the rays. MacDougall brought about mutations in *Chilodonella* by means of these rays (p. 164). When ciliates are vitally stained with eosin, erythrosin, etc., they react sometimes positively or negatively, as in *Paramecium* (Metzner), or always negatively, as in *Spirostomum* (Blättner). According to Efimoff, this "induced phototaxis" is not limited to fluorescent dyes, but also is possessed by all vital-staining dyes. Zuelzer (1905) studied the effects of radium rays upon various Protozoa and found that the effect was not the same among different species. For example, limax amoeba was more resistant than others. In all cases, however, long exposure to the rays was fatal to Protozoa, the first effect of exposure being shown by accelerated movement. Halberstaedter and Luntz (1929) studied injuries and death of *Eudorina elegans* by exposure to radium rays. Joseph and Prowazek (1902) found *Paramecium* and *Volvox* gave negative response to the röntgen-ray.

Reaction to temperature stimuli. As was stated before, there seems to be an optimum temperature range for each protozoan, although it can withstand temperatures which are lower or higher than that range. As a general rule, the higher the temperature, the greater the metabolic activities, and the latter condition results in turn in a more rapid growth and more frequent reproduction. It has been suggested that change to different phases in the life-cycle of a protozoan in association with the seasonal change may be largely due to temperature changes of the environment. In the case of parasitic Protozoa which pass their life-cycle in warm-blooded and cold-blooded host animals, such as *Plasmodium* and mammalian trypanosomes, the change in body temperature of host animals may bring about specific stages in their development.

Reaction to electrical stimuli. Since Verworn's experiments, several investigators studied the effects of electric current which is passed through Protozoa in water. Amoeba shows negative reaction to the anode and moves toward the cathode either by reversing the cytoplasmic streaming (Verworn) or by turning around the body (Jennings). The free-swimming ciliates move mostly toward the cathode, but a few may take a transverse

position (*Spirostomum*) or swim to the anode (*Paramecium*, *Stentor*, etc.). Of flagellates, Verworn noticed that *Trachelomonas* and *Peridinium* moved to the cathode, while *Chilomonas*, *Cryptomonas*, and *Polytomella*, swam to the anode.

Regeneration

The power of regenerating the lost parts of the body is characteristic of all Protozoa from simple forms to those with highly complex organization, as shown by observations of numerous investigators. The general procedure of the experiment is to cut the body of a protozoan into two or more parts and observe how far each part regenerates. It is now well established that only the parts which contain the whole or part of the nucleus are able to regenerate completely under favorable circumstances. A remarkably small portion of a protozoan is known to regenerate completely. For example, Sokoloff found 1/53–1/69 of *Spirostomum* and 1/70–1/75 of *Dileptus* were able to regenerate. According to Philps, portions down to 1/80 of an amoeba are able to regenerate. Burnside (1929) cut 27 specimens of *Stentor coeruleus* belonging to a single clone, into two or more parts in such a way that some of the pieces contained a large portion of the nucleus while others a small portion. These fragments regenerated and multiplied, giving rise to 268 individuals. No dimensional differences resulted from the different amounts of nuclear material present in the cut specimens. Apparently regulatory processes took place and in all cases normal size was restored, no matter what was the amount of the nuclear material in ancestral pieces. Thus, in this ciliate, biotypes of diverse size are not produced by causing inequalities in the proportions of nuclear material in different individuals.

The parts which do not contain nuclear material, may continue to show certain activities, such as locomotion, contraction of the contractile vacuole, etc., for some time. For example, Penard observed enucleated amoebae lived eight days, Stole and Gruber found amoebae without nuclear material were able to live up to 30 days, and enucleated pieces of *A. verrucosa* were seen to remain alive for 20 to 25 days (Grosse-Allermann).

At the time of reproduction of all Protozoa, the various organelles, such as cilia, flagella, cytostome, contractile vacuole, etc., are completely regenerated before the separation of body occurs.

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CHAPTER 5

Reproduction

THE mode of reproduction in Protozoa is highly variable among different groups, although it is primarily a cell division. The reproduction is initiated by the nuclear division in all cases, which will therefore be considered first.

Nuclear division

Between a simple direct division on the one hand and a complicated indirect division which is comparable with the typical metazoan mitosis on the other hand, all types of nuclear division are to be encountered.

Direct nuclear division. While not so widely found as it was thought to be in former years, amitosis occurs normally and regularly in many forms. The macronuclear division of the Ciliophora is without exception direct. The macronucleus elongates itself without any particular changes in its internal structure and becomes divided through the middle, resulting in formation of two daughter nuclei as seen commonly in *Paramecium* (Fig. 48).

It is assumed that the nuclear components undergo solation during division, since the formed particles of nucleus which are stationary in the resting stage, manifest a very active Brownian movement as was observed *in vivo* in *Endamoeba blattae* (Fig. 49). Furthermore, in some cases the nuclear components may undergo phase reversal, that is to say, the chromatin granules which are dispersed phase in the non-staining fluid dispersion medium in the resting nucleus, become dispersion medium in which the latter is suspended as dispersed phase. By using Feulgen's nucleal reaction, Reichenow (1928) demonstrated this reversal phenomenon in the division of the macronucleus of *Chilodonella cucullulus* (Fig. 50).

When the macronucleus is elongated as in *Spirostomum*, *Stentor*, *Euplotes*, etc., the nucleus becomes condensed into a rounded form prior to its division. When the macronuclear material is distributed throughout the cytoplasm as numerous grains as in *Dileptus anser* (Fig. 239, c), "each granule divides where it happens to be and with the majority of granules both halves

remain in one daughter cell after division" (Calkins). Hayes noticed a similar division, but at the time of simultaneous division prior to cell division, each macronucleus become elongated and breaks into several small nuclei.

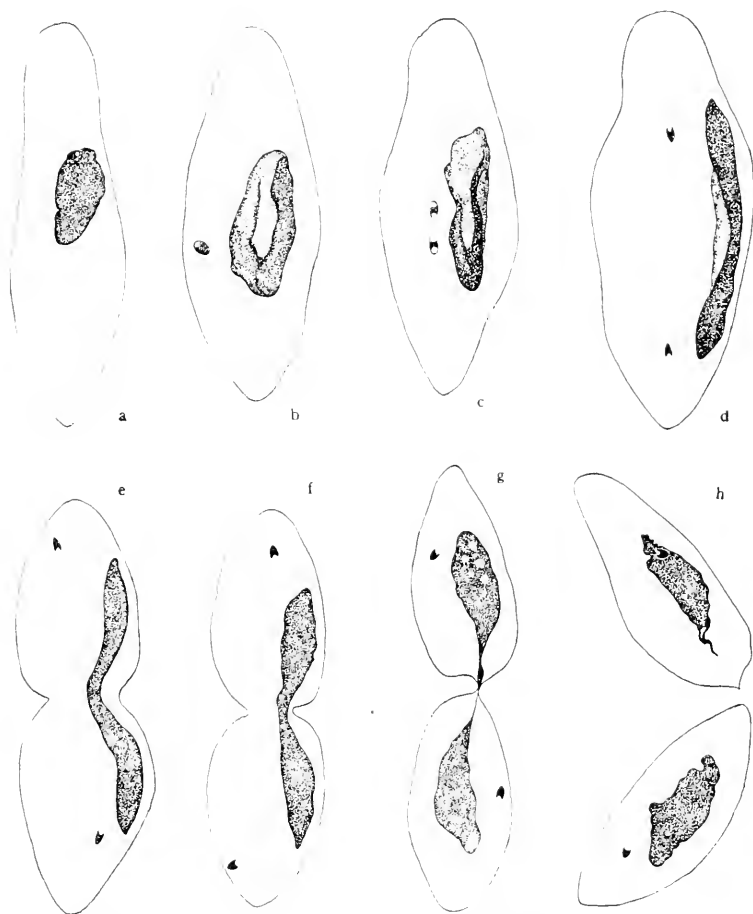


FIG. 48. Nuclear and cytosomic division of *Paramecium caudatum* as seen in stained smears, $\times 260$ (Kudo).

The macronucleus becomes at the time of its division somewhat enlarged and its chromatin granules are more deeply stained than before. Since the number of chromatin granules appear approximately the same in the macronuclei of different generations

of a given species, the reduced number of chromatin granules must be restored sometime before the next division takes place. Calkins (1926) is of the opinion that "each granule elongates and divides into two parts, thus doubling the number of chromo-

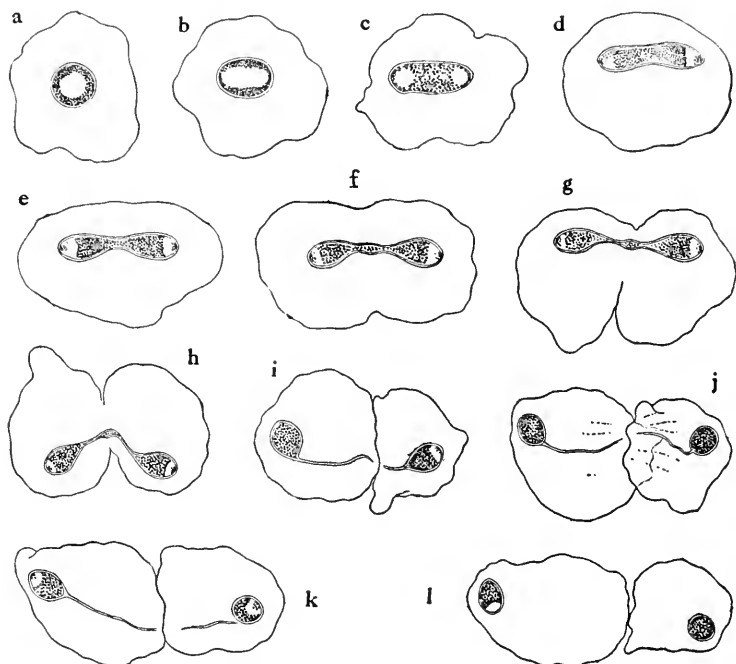


FIG. 49. Division of *Endamoeba blattae* as seen in life, $\times 250$ (Kudo).
The entire process took one hour and seven minutes.

meres." Reichenow (1928) found that in *Chilodonella cucullulus* the lightly Feulgen positive endosome appeared to form chromatin granules and Kudo (1936) maintained that the large chromatin spherules of the macronucleus of *Nyctotherus ovalis* probably produce smaller spherules in their alveoli.

In the elongated or miniliform macronuclei of a number of ciliates, there occur, prior to and during division, 1–2 characteristic zones which have been called by various names, such as nuclear clefts, reconstruction bands, reorganization bands, etc. In *Euplotes patella*, Turner (1930) observed before division, a reorganization band consisting of an unstained zone ("reconstruc-

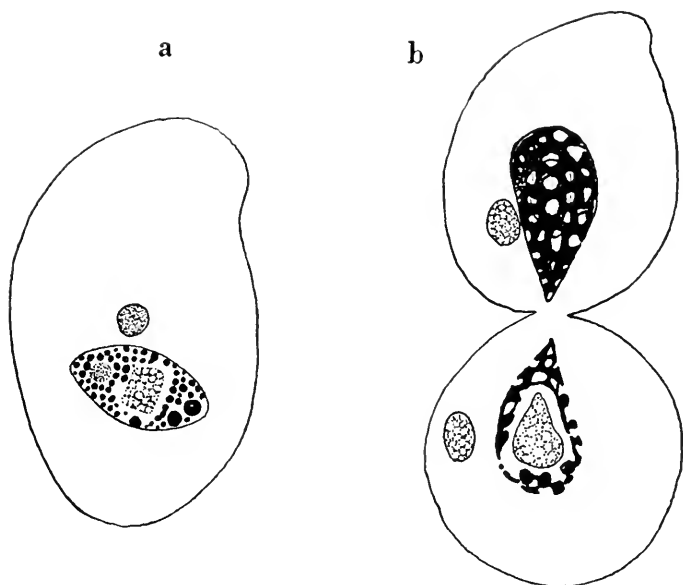


FIG. 50. The solation of chromatin during the macronuclear division of *Chilodonella cucullulus*, positive to Feulgen's nucleal reaction, $\times 1800$ (Reichenow).

tion plane") and a stained zone ("solution plane"), appears at each end of the macronucleus (Fig. 51, *a*) and as each moves toward the middle, a more chromatinic area is left behind (*b-d*). According to Summers (1935), a similar change occurs in *Dio-*

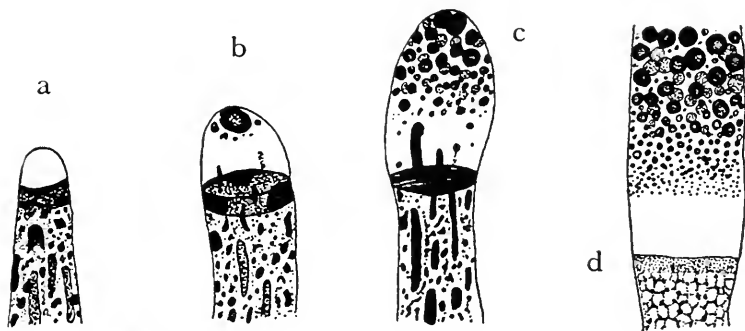


FIG. 51. Macronuclear reorganization before division in *Euplotes patella*, $\times 240$ (Turner). *a*, reorganization band appearing at a tip of the macronucleus; *b-d*, later stages.

phrys appendiculata and *Stylonychia pustulata*; but in *Aspidisca lynceus* (Fig. 52) a reorganization band appeared first near the middle region of the macronucleus (b), divided into two and each moved toward an end, leaving between them a greater chromatinic contents of the reticula (c-i). Summers suggested that "the

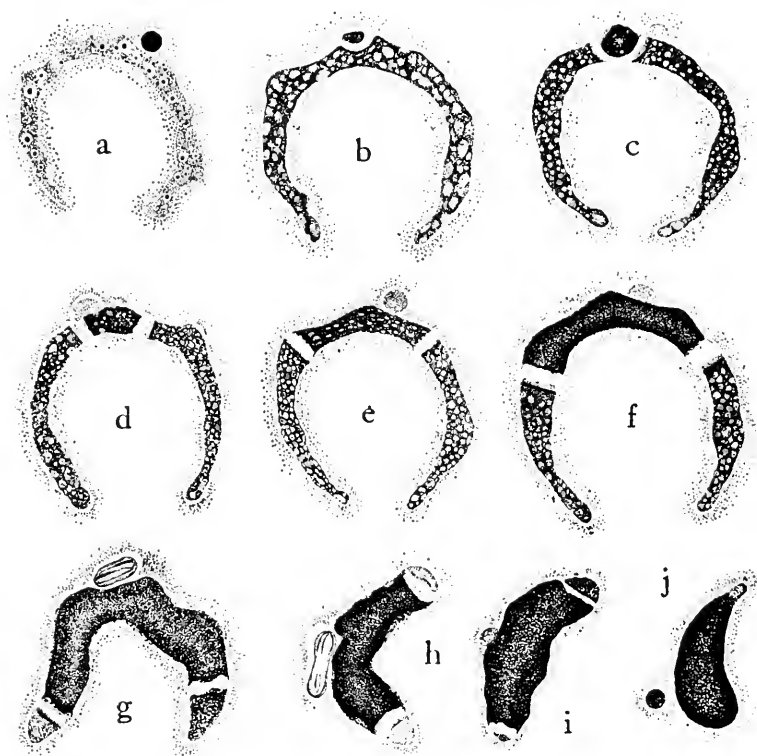


FIG. 52. Macronuclear reorganization prior to division in *Aspidisca lynceus*, $\times 1400$ (Summers). a, resting nucleus; b-i, successive stages in reorganization process; j, a daughter macronucleus shortly after division.

reorganization bands are local regions of karyolysis and re-synthesis of macronuclear materials with the possibility of an elimination of physically or possibly chemically modified non-staining substances into the cytoplasm."

The discarding of a certain portion of the macronuclear material during division has been observed in a number of species.

In *Uroleptus halseyi*, Calkins actually noticed each of the eight macronuclei is "purified" by discarding a reorganization band and an "x-body" into the cytoplasm before fusing into a single macronucleus which then divides into two nuclei. In the more or less rounded macronucleus which is commonly found in many ciliates, no reorganization band has been recognized. A number of observers have however noted during the nuclear division there appears and persists a small body within the nuclear figures,

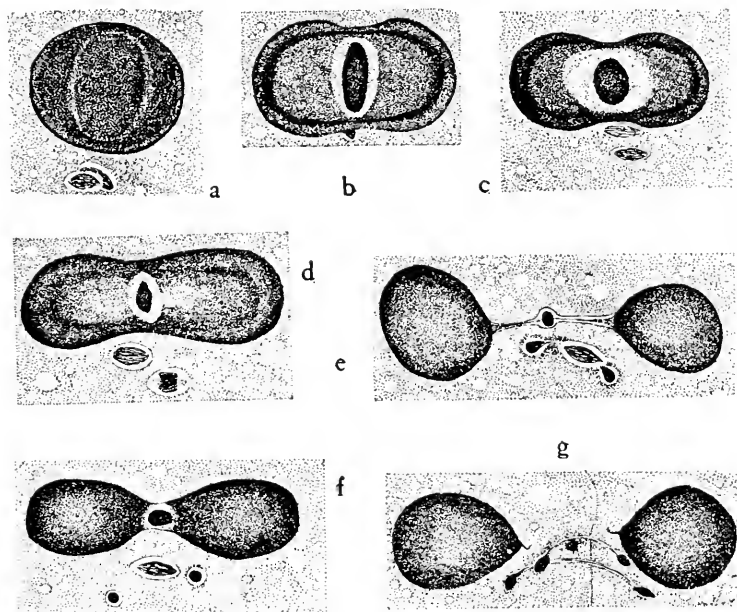


FIG. 53. Macronuclear division in *Conchophthirus mytili*,
 ×440 (Kidder).

located at the division plane as in the case of *Loxocephalus* (Behrend), *Eupoterion* (MacLennan and Connell) and even in the widely different protozoan, *Endamoeba blattae* (Kudo) (Fig. 49). We owe Kidder for a careful comparative study of this body. Kidder (1933) observed that during the division of the macronucleus of *Conchophthirus mytili* (Fig. 53), the nucleus "casts out a part of its chromatin at every vegetative division," which "is broken down and disappears in the cytoplasm of either daughter organism." A similar phenomenon has since been found

further in *C. anodontae*, *C. curtus*, *C. magna* (Kidder), *Urocentrum turbo*, *Colpidium colpoda*, *C. campylum*, *Glaucoma scintillans* (Kidder and Diller), and *Allosphaerium convexa* (Kidder and Summers). Kidder and his associates believe that the process is probably elimination of waste substances of the prolonged cell-division, since chromatin extrusion does not take place during a few divisions subsequent to reorganization after conjugation in *Conchophthirus mytili* and since in *Colpidium* and *Glaucoma*, the chromatin elimination appears to be the cause of high division rate and infrequency of conjugation.

Other examples of amitosis are found in the vesicular nuclei in the trophozoite of Myxosporidia, as for example, *Myxosoma catostomi* (Fig. 54), *Thelohanellus notatus* (Debaisieux), etc., in which the endosome divides first, followed by the nuclear constriction. In *Streblomastix strix*, the compact elongated nucleus was found to undergo a simple division by Kofoid and Swezy.

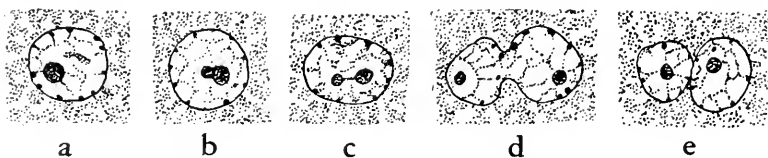


FIG. 54. Amitosis in the trophozoite of *Myxosoma catostomi*, $\times 2250$ (Kudo).

Indirect nuclear division. The indirect division which occurs in the protozoan nuclei is of manifold types as compared with the mitosis in the metazoan cell, in which, aside from minor variations, the change is of a uniform pattern. Chatton, Alexieff and others, have proposed several terms to designate the various types of indirect nuclear division, but no one of these types is sharply defined. For our purpose, mentioning of examples will suffice.

A veritable mitosis was noted by Dobell in the heliozoan *Oxnerella maritima* (Fig. 55), which possesses an eccentrically situated nucleus containing a large endosome and a central centriole, from which radiate many axopodia (*a*). The first sign of the nuclear division is the slight enlargement, and migration toward the centriole, of the nucleus. The centriole first divides into two (*c*, *d*) and the nucleus becomes located between the two centrioles (*e*). Presently spindle fibers are formed

and the nuclear membrane disappears (*f*, *g*). After passing through an equatorial-plate stage, the two groups of the chromosomes move toward the opposite poles (*g*–*i*). As the spindle fibers become indistinct, radiation around the centrioles becomes conspicuous and the two daughter nuclei are completely recon-

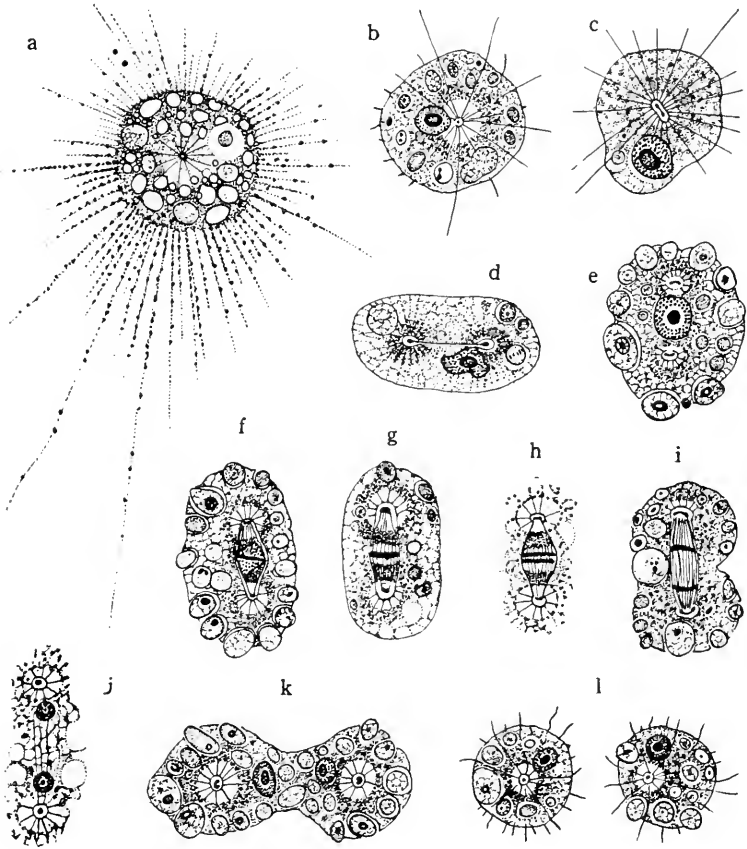


FIG. 55. Nuclear and cytosomic division in *Oxnerella maritima*, \times about 1000 (Dobell). a, a living individual; b, stained specimen; c–g, prophase; h, metaphase; i, anaphase; j, k, telophase; l, division completed.

structed to assume the resting phase (*j*–*l*). The mitosis of another heliozoan *Acanthocystis aculeata* is, according to Schaudinn and Stern, very similar to the above. Aside from these two species,

the centriole has been reported in many others, such as *Hartmannella* (Arndt), *Euglypha*, *Monocystis* (Bělař), *Aggregata* (Dobell, Bělař, and Naville), various *Hypermastigina* (Kofoid; Duboseq, Grassé; Kirby; Cleveland and his associates).

In numerous species the division of the centriole (or blepharoplast) and a connecting strand between them, which have been called **desmose**, centrodsmose or paradesmose, have been observed. According to Kofoid and Swezy (1919), in *Trichonympha campanula* (Fig. 56), the prophase begins early, during which 52 chromosomes are formed and become split. The nucleus moves nearer the anterior end where the centriole divides into two, between which develops a desmose. From the posterior end of each centriole, astral rays extend out and the split chromosomes form loops, pass through "tangled skein" stage, and emerge as 26 chromosomes. In the metaphase, the equatorial plate is made up of V-shaped chromosomes as each of the split chromosomes are still connected at one end, which finally becomes separate in anaphase, followed by formation of two daughter nuclei.

As to the origin and development of the achromatic figure, various observations and interpretations have been advanced. Certain *Hypermastigina* possess very large filiform centrioles and a large rounded nucleus. In *Barbulanympha* (Fig. 57), Cleveland (1938) found that the **centrioles** vary from 15 to 30 μ in length in the four species of the genus which he studied. They can be seen, according to Cleveland, in life as made up of a dense hyaline protoplasm. When stained, it becomes apparent that the two centrioles are joined at their anterior ends by a **desmose** and their distal ends 20 to 30 μ apart, each of which is surrounded by a special **centrosome** (*a*). In the resting stage no fibers extend from either centriole, but in the prophase, astral rays begin to grow out from the distal end of each centriole (*b*). As the rays grow longer (*c*), the two sets soon meet and the individual rays or fibers join, grow along one another and overlap to form the **central spindle** (*d*). In the resting nucleus, there are large irregular chromatin granules which are connected by fibrils with one another and also with the nuclear membrane. As the achromatic figure is formed and approaches the nucleus, the chromatin becomes arranged in a single spireme imbedded in matrix. The spireme soon divides longitudinally and the double spireme presently breaks up transversely into paired chromosomes. The

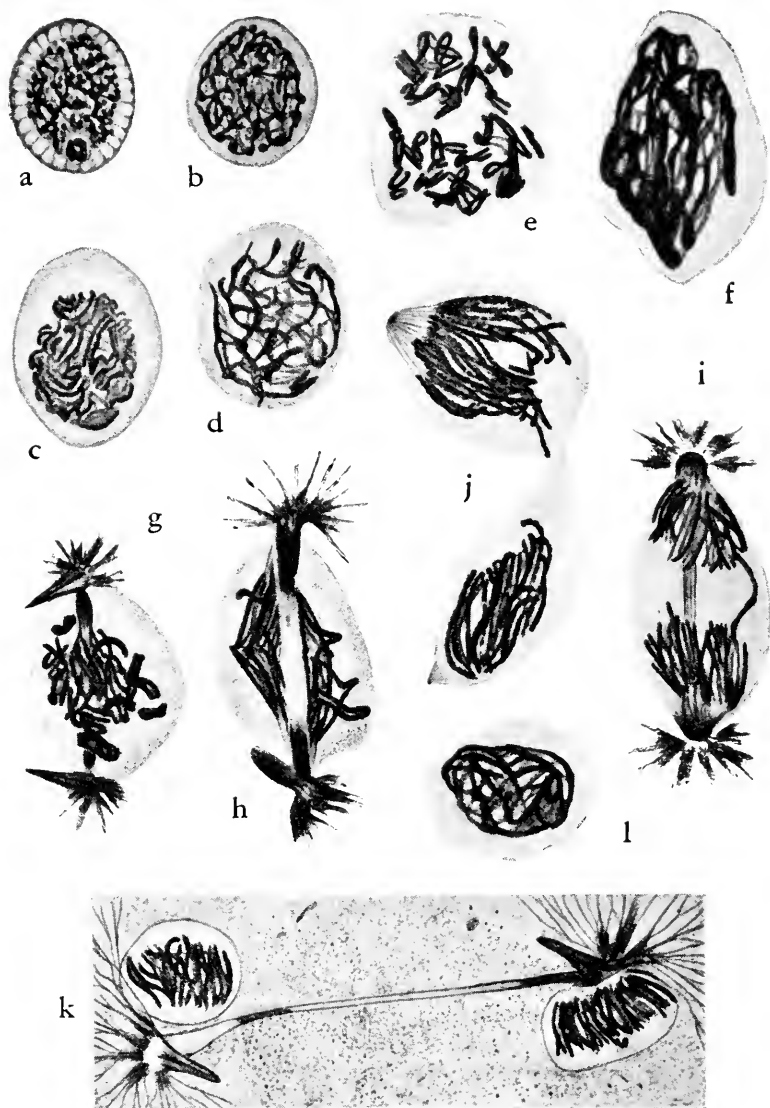


FIG. 56. Mitosis in *Trichonympha campanula*, $\times 800$ (Kofoed and Swezy). a, resting nucleus; b-g, prophase; h, metaphase; i, j, anaphase; k, telophase; l, a daughter nucleus being reconstructed.

central spindle begins to depress the nuclear membrane and the chromosomes become shorter and move apart. The intra- and

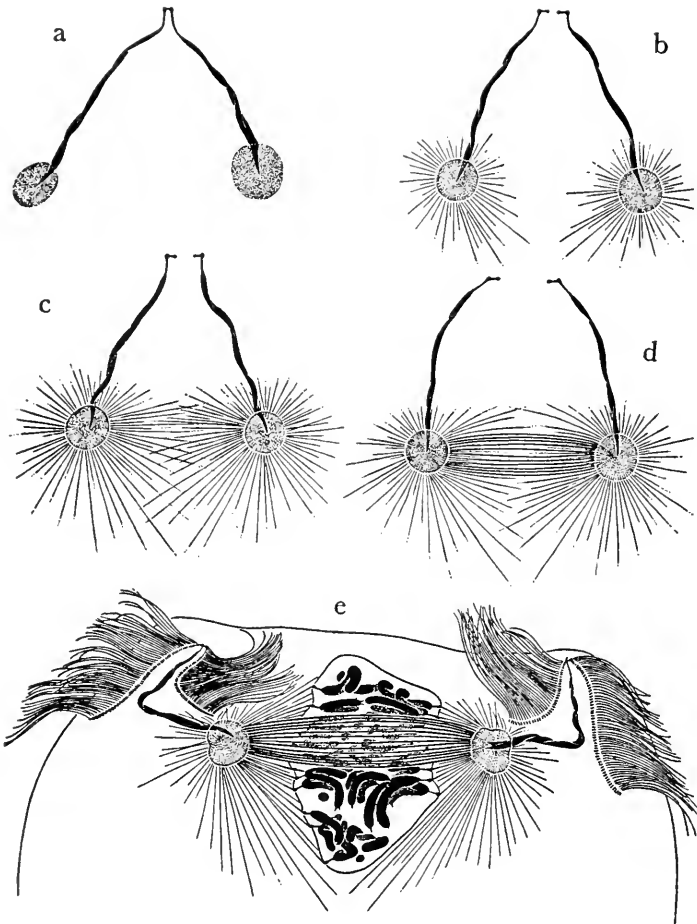


FIG. 57. Development of spindle and astray rays during the mitosis in *Barbulanympha*, $\times 930$ (Cleveland). a, interphase centrioles and centrosomes; b, prophase centrioles with astral rays developing from their distal ends through the centrosomes; c, meeting of astral rays from two centrioles; d, astral rays developing into the early central spindle; e, a later stage showing the entire nuclear figure.

extranuclear fibrils unite as the process goes on (e), the central spindle now assumes an axial position, and two groups of V-shaped chromosomes are drawn to opposite poles. In the telophase, the chromosomes elongate and becomes branched, thus assuming conditions seen in the resting nucleus.

In the unique resting nucleus of *Spirotrichonympha polygyra* (Fig. 58), Cleveland (1938) found four chromosomes, each of which contains a distinct coil within a sheath and its one end connected with the anterior margin of the nuclear membrane by an

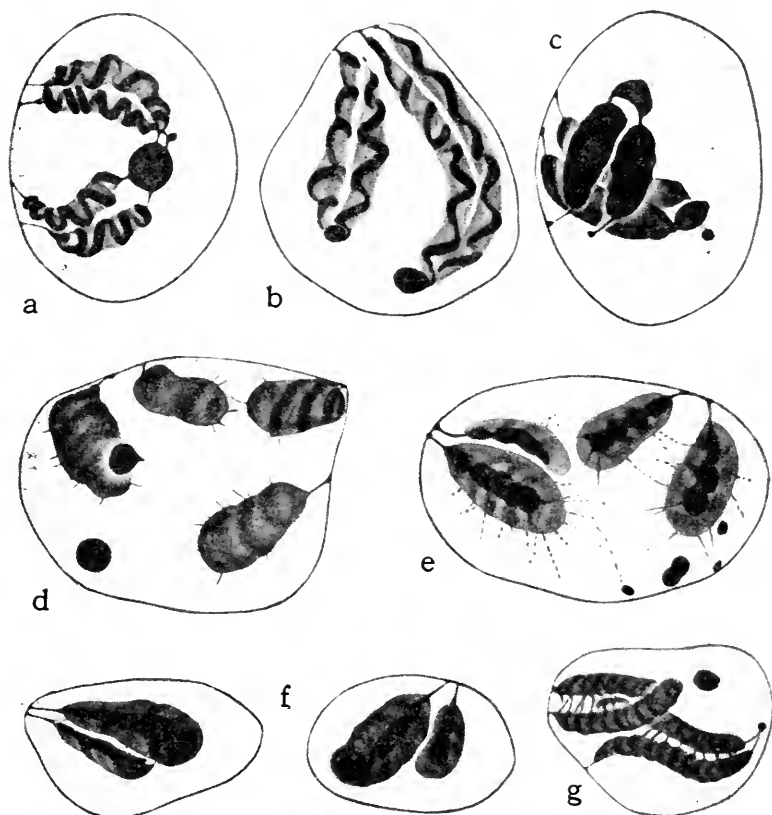


FIG. 58. Mitosis in *Spirotrichonympha polygyra* (Cleveland). a, resting nucleus with 4 chromosomes; b, c, prophase; d, chromosomes moving apart; e, elongation of nucleus; f, telophase; g, a daughter nucleus in which the chromosomes are splitting. a-e, $\times 3800$; f, g, $\times 2400$.

intranuclear chromosomal fiber, and the other with a deeply staining endosome (a). The spindle fibers appear between the separating flagellar bands which come in contact with the nuclear membrane. Soon some of the astral rays become connected with the intranuclear chromosomal fibers and one long and one short

chromosomes which become thicker and shorter move toward each pole. During the telophase, each chromosome splits lengthwise and forms the resting nucleus (*g*). In *Lophomonas blattarum*, the nuclear division (Fig. 59) is initiated by the migration of the nucleus out of the calyx. On the nuclear membrane is attached the centriole which probably originates in the blepharoplast ring;

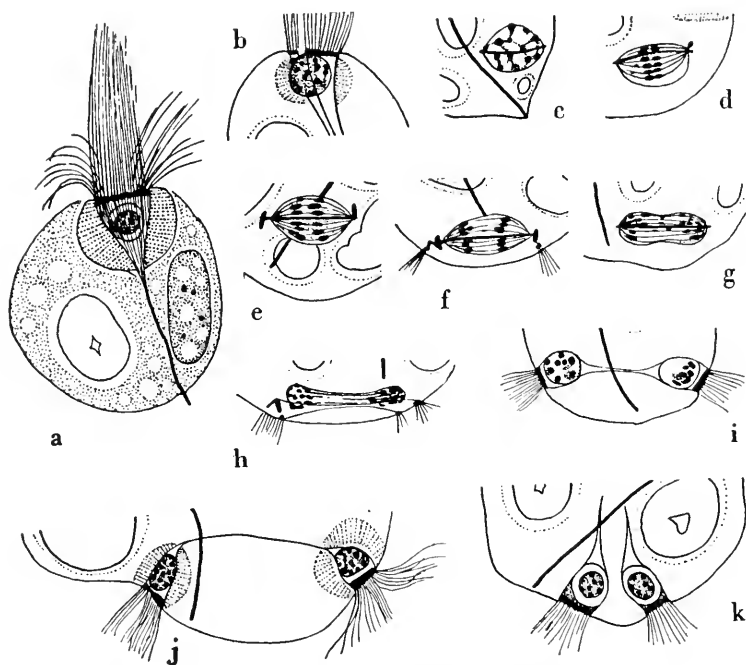


FIG. 59. Nuclear division in *Lophomonas blattarum*, $\times 1530$ (Kudo), a, resting nucleus; b, c, prophase; d, metaphase; e-h, anaphase; i-k, telophase.

the centriole divides and the desmose which grows, now stains very deeply, the centrioles becoming more conspicuous in the anaphase when new flagella develop from them. Chromatin granules become larger and form a spireme, from which 6-8 chromosomes are produced. Two groups of chromosomes move toward the opposite poles, and when the division is completed, each centriole becomes the center of formation of all motor organellae.

In some forms, such as *Noctiluca* (Calkins), *Actinophrys* (Bělař), etc., there may appear at each pole, a structureless mass of cytoplasm (centrosphere), but in a very large number of species there appear no special structures at poles and the spindle fibers become stretched seemingly between the two extremities of the elongating nuclear membrane. Such is the condition found in *Cryptomonas* (Bělař), *Rhizochrysis* (Doflein), *Aulacantha* (Borgert), and in micronuclear division of the majority of *Euciliata* and *Suctorina*.

The behavior of the endosome during the mitosis differs among different species as are probably their functions. In *Eimeria schubergi* (Schaudinn), *Euglena viridis* (Tschenzoff), *Oxyrrhis marina* (Hall), *Colacium vesiculosum* (Johnson), *Haplosporidium limnodrili* (Granata), etc., the conspicuously staining endosome divides by elongation and constriction along with other chromatic elements, but in many other cases, it disappears during the early part of division and reappears when the daughter nuclei are reconstructed as observed in *Monocystis*, *Dimorpha*, *Euglypha*, *Pamphagus* (Bělař), *Acanthocystis* (Stern), *Chilomonas* (Doflein), *Dinenympha* (Kirby), etc.

In the vegetative division of the micronucleus of *Conchophthirus anodontae* (Fig. 60), Kidder (1934) found that prior to division the micronucleus moves out of the pocket in the macronucleus and the chromatin becomes irregularly disposed in a reticulum; swelling continues and the chromatin condenses into a twisted band, a spireme, which breaks into many small segments, each composed of large chromatin granules. With the rapid development of the spindle fibers, the twelve bands become arranged in the equatorial plane and condense. Each chromosome now splits longitudinally and two groups of 12 daughter chromosomes move to opposite poles and transform themselves into two compact daughter nuclei. In *Zelleriella intermedia* (Fig. 61), Chen (1936) saw the formation of 24 chromosomes, each of which is connected with a fiber of the intranuclear spindle and splits lengthwise in the metaphase. While in the majority of protozoan mitosis, the chromosomes split longitudinally, there are observations which suggest a transverse division. As examples may be mentioned the chromosomal divisions in *Astasia laevis* (Bělař), *Entosiphon sulcatum* (Lackey), and a number of ciliates. In a small number of species observations vary, as, for example, in

Peranema trichophorum in which the chromosomes were observed to divide transversely (Hartmann and Chagas) as well as longitudinally (Hall and Powell; Brown). It is inconceivable that the division of the chromosome in a single species of organism is haphazard. The apparent transverse division might be explained

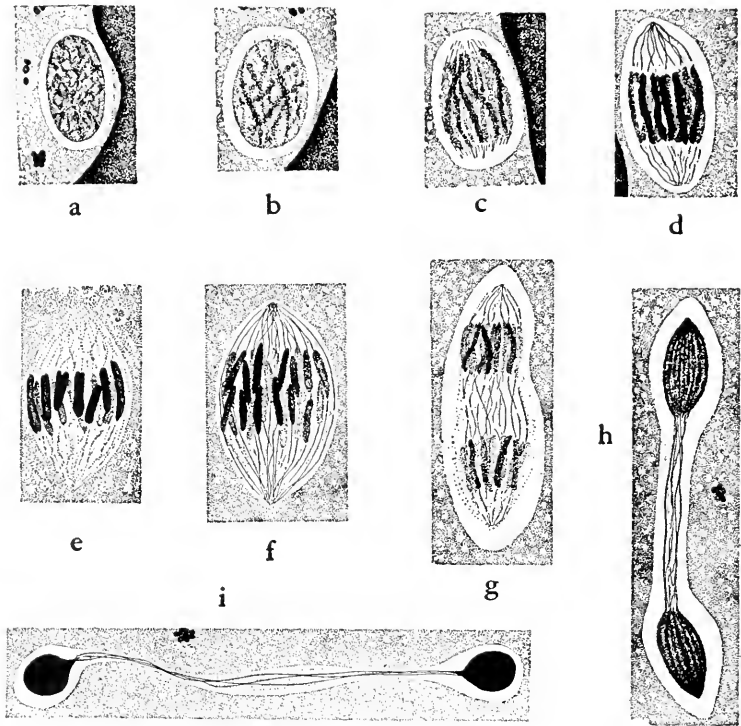


FIG. 60. Mitosis of the micronucleus of *Conchophthirus anodontae*, $\times 2640$ (Kidder). a-c, prophase; d, e, metaphase; f, g, anaphase; h, i, telophase.

by assuming, as Hail (1937) showed in *Euglena gracilis*, that the splitting is not completed at once and the pulling force acting upon them soon after division brings forth the long chromosomes still connected at one end. Thus the chromosomes remain together before the anaphase begins.

In the instances considered on the preceding pages, the so-called chromosomes found in them, appear to be essentially

similar in structure and behavior to typical metazoan chromosomes. In many other cases, the so-called chromosomes or "pseudochromosomes" are slightly enlarged chromatin granules which differ from the ordinary chromatin granules in their time of appearance and movement only. In these cases it is of course

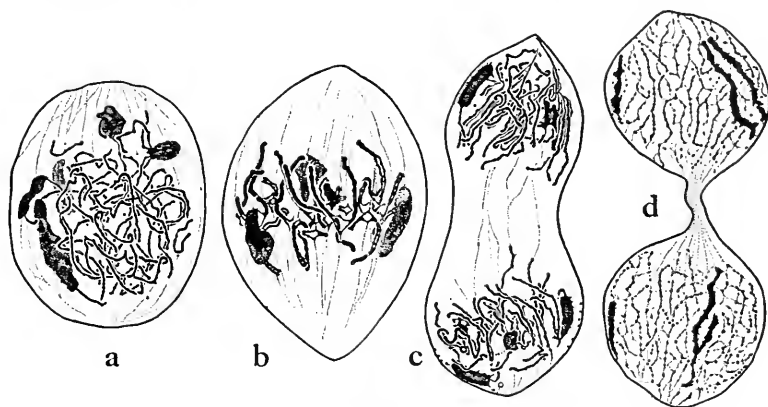


FIG. 61. Stages in mitosis in *Zelleriella intermedia*, $\times 1840$ (Chen).
a, early prophase; b, metaphase; c, anaphase; d, telophase.

not possible at present to determine how and when their division occurs before separating to the respective division pole. In the following table are listed the number of the "chromosomes" which have been reported by various investigators in the Protozoa that are mentioned in the present work:

Protozoa	Number of chromosomes	Observers
<i>Rhizochrysis scherffeli</i>	22	Doflein
<i>Haematococcus pluvialis</i>	20-30	Elliott
<i>Polytomella agilis</i>	5	Doflein
<i>Chlamydomonas</i> spp.	10 (haploid)	Pascher
<i>Euglena pisciformis</i>	12-15(?)	Dangeard
<i>E. viridis</i>	30 or more	Dangeard
<i>Phacus pyrum</i>	30-40	Dangeard
<i>Menoidium incurvum</i>	About 12	Hall
<i>Vacuolaria virescens</i>	About 30	Fott
<i>Syndinium turbo</i>	5	Chatton
<i>Anthophytha vegetans</i>	8-10	Dangeard
<i>Cercomonas longicauda</i>	4-5	Dangeard
<i>Collodictyon triciliatum</i>	About 20	Bělař

Protozoa	Number of chromosomes	Observers
<i>Chilomastix gallinarum</i>	About 12	Boeck and Tanabe
<i>Eutrichomastix serpentis</i>	5	Kofoid and Swezy
<i>Dinenympha fimbriata</i>	25-30	Kirby
<i>Metaderescorina debilis</i>	About 4	Light
<i>Trichomonas clongatum</i>	3	Hinsshaw
<i>T. batrachorum</i>	4 or 8	Kuczynski
	6	Bishop
<i>T. augusta</i>	6	Bishop
<i>Hexamita salmonis</i>	5 or 6	Davis
<i>Giardia intestinalis</i>	4	Kofoid and Swezy
<i>G. muris</i>	4	Kofoid and Christensen
<i>Calonympha grassii</i>	4 or 5	Janiecki
<i>Spirotrichonympha polygyra</i>	2 doubles	Cup
	2	Cleveland
<i>Lophomonas blattarum</i>	16 or 8 doubles	Janiecki
	8 or 6	Kudo
	12 or 6 doubles	Bělař
<i>L. striata</i>	12 or 6 doubles	Bělař
<i>Barbulanympha laurabuda</i>	40	Cleveland
<i>B. ufalula</i>	50	Cleveland
<i>Rhynchonympha tarda</i>	19	Cleveland
<i>Urinympha tulca</i>	14	Cleveland
<i>Staurojoenia assimilis</i>	24	Kirby
<i>Trichonympha campanula</i>	52 or 26 doubles	Kofoid and Swezy
<i>T. grandis</i>	22	Cleveland
<i>Dimastigamoeba bistadiatis</i>	16-18	Kühn
<i>Endamoeba disparata</i>	About 12	Kirby
<i>Entamoeba histolytica</i>	6	Kofoid and Swezy; Uribe
<i>E. coli</i>	6	Swezy; Stabler
<i>Hydramoeba hydroxena</i>	8	Reynolds and Threlkeld
<i>Actinophrys sol</i>	44 (diploid); 22 (haploid)	Bělař
<i>Oxnerella maritima</i>	About 24	Dobell
<i>Thalassicolla nucleata</i>	4	Bělař
<i>Aulacantha scolymantha</i>	More than 1600	Borgert
	4 in gamogony	Bělař
<i>Zygosoma globosum</i>	12 (diploid); 6 (haploid)	Noble
<i>Diplocystis schneideri</i>	6 (diploid); 3 (haploid)	Jameson

Protozoa	Number of chromosomes	Observers
<i>Nina gracilis</i>	5 (haploid)	Léger and Duboseq
<i>Aggregata eberthi</i>	12 (diploid); 6 (haploid)	Dobell and Jameson; Bělař; Naville
<i>Adlea ovata</i>	8-10 (diploid); 4-5 (haploid)	Greiner
<i>Orcheobius herpobdellae</i>	10-12	Kunze
<i>Chloromyxum leydigi</i>	4 (diploid); 2 (haploid)	Naville
<i>Myxidium lieberkuhni</i>	4	Bremer
<i>Sphaeromyxa sabrazesi</i>	6	Debaisieux; Bělař
	4	Naville
<i>S. balbiani</i>	4	Naville
<i>Myxobolus pfeifferi</i>	4	Keysselitz; Mercier; Georgevitch
<i>Protoopalina intestinalis</i>	8 (diploid); 4 (haploid)	Metcalf
<i>Zelleriella antilliensis</i>	2(?)	Metcalf
<i>Z. intermedia</i>	24	Chen
<i>Didinium nasutum</i>	16 (diploid); 8 (haploid)	Prandtl
<i>Chilodonella uncinata</i>	4 (diploid); 2 (haploid)	Enrique; McDougall
<i>C. uncinata</i> (tetraploid)	8; 4	McDougall
<i>Conchophthirus anodontae</i>	12 (diploid)	Kidder
<i>C. mytili</i>	16 (diploid); 8 (haploid)	Kidder
<i>Ancistruma isseli</i>	About 5 (haploid)	Kidder
<i>Paramecium aurelia</i>	30-40	Diller
<i>Stentor coeruleus</i>	28 (diploid); 14 (haploid)	Mulsow
<i>Oxytricha fallax</i>	24 (diploid); 12 (haploid)	Gregory
<i>Uroleptus halseyi</i>	24 (diploid); 12 (haploid)	Calkins
<i>Pleurotricha lanceolata</i>	About 40 (dipl.); 20 (hapl.)	Manwell
<i>Stylonychia pustulata</i>	6	Prowazek
<i>Euplotes patella</i>	6 (diploid)	Yocom; Ivanic
	8 (diploid); 4 (haploid)	Turner
<i>Carchesium polypinum</i>	16 (diploid); 8 (haploid)	Popoff
<i>Trichodina</i> sp.	4-6	Diller

In many other Protozoa, the division figure, especially the achromatic figure, suggests strongly a mitosis, but the chromatin substance which makes up the equatorial plate can hardly be called chromosomes. A typical example of this type is found in the nuclear division of *Amoeba proteus* (Fig. 62). According to Chalkley and Daniel (1933), the conspicuous granules present in the resting nucleus, under the membrane contain very little chromatin, while abundant chromatin is lodged in the central

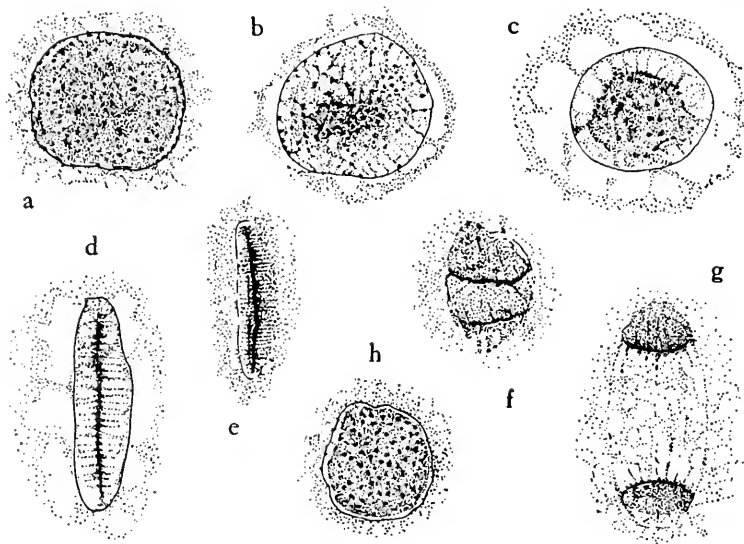


FIG. 62. Nuclear division in *Amoeba proteus*, $\times 180$ (Chalkley and Daniel). a, resting stage; b-d, prophase; e, metaphase; f, g, anaphase; h, a daughter nucleus.

area. The peripheral granules appear to give rise to achromatic figure. At the beginning of division, the chromatin granules become aggregated in a zone (b); they then assume a ring-form along the periphery of the central mass of network (c); at this stage, the cytoplasm around the nucleus is much vacuolated. A little later appears a discoid equatorial plate or ring which is connected with the nuclear membrane by numerous fibrils, and the nucleus becomes markedly flattened with its membrane still intact (d), which is considered as the end of the prophase. In the metaphase, the nuclear membrane becomes extremely faint and the portion over one side of the plate is without it (e). At the

anaphase the membrane completely disappears, the equatorial plate splits and each half contracts in the plane of the plate, producing two daughter-plates. In some specimens a faint spindle formation was noted. At about this time, vacuolated condition of the perinuclear cytoplasm disappears (*f*). In later phases of anaphase the plates are more widely separated and are slightly less in diameter as compared with earlier stages. There are distinct polar caps of fibrillar material at the poles of the spindle (*g*), finally each plate transforms itself into a resting nucleus (*h*). The two investigators added that if the chromatin granules located in the equatorial plate are chromosomes, "they must be extremely numerous." Liesche (1938) recently estimates the number of these granules which he called chromosomes as between 500 and 600.

Cytosomic division

Binary fission. As in metazoan cells, the binary fission occurs very widely among the Protozoa. It is a division of the body through middle of the extended long axis into two nearly equal daughter individuals (Fig. 49). In *Amoeba proteus*, Chalkley and Daniel found that there is a definite correlation between the stages of nuclear division and external morphological changes (Fig. 63). During the prophase, the organism is rounded, studded with fine pseudopodia and exhibits under reflected light a clearly defined hyaline area at its center (*a*), which disappears in the metaphase (*b*, *c*). During the anaphase the pseudopodia rapidly become coarser; in the telophase the elongation of body, cleft formation, and return to normal pseudopodia, take place.

In Testacea, one of the daughter individuals remains, as a rule, within the old test, while the other moves into a newly formed one, as in *Arcella*, *Pyxidicula*, *Euglypha*, etc. According to Doflein, the division plane coincides with the axis of body in *Cochliopodium*, *Pseudodiffugia*, etc., and the delicate homogeneous test also divides into two parts. In the majority of the *Mastigophora*, the division is longitudinal, as is shown by that of *Menoidium incurvum* (Fig. 64). In certain dinoflagellates, such as *Ceratium*, *Cochliodinium*, etc., the division plane is oblique, while in forms such as *Oxyrrhis* (Dunkerly; Hall), the fission is transverse. In *Streblomastix strix* (Kofoid and Swezy), *Lophomonas striata* (Kudo), *Spirotrichonympha bispira* (Cleveland), etc., the division takes place transversely but the polarity of the

posterior individual is reversed so that the posterior end of the parent organism becomes the anterior end of the posterior daughter individual. In the ciliate *Bursaria*, Lund (1917), observed reversal of polarity in one of the daughter organisms at the time of division of normal individuals and also in those which regenerated after being cut into one-half the normal size.

In the Ciliophora the division is as a rule transverse (Fig. 48),

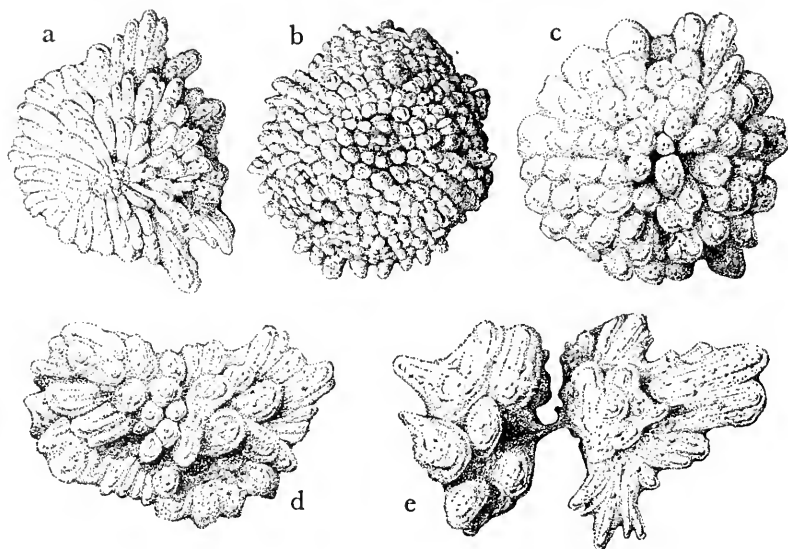


FIG. 63. External morphological changes during division of *Amoeba proteus*, as viewed in life in reflected light, \times about 20 (Chalkley and Daniel). a, shortly before the formation of the division sphere; b, a later stage; c, prior to elongation; d, further elongation; e, division almost completed.

in which the cytostome without any enlargement or elongation divides by constriction through the middle so that the two daughter individuals are about half as large at the end of division. Both individuals retain their polarity except in a few cases.

Multiple division. In multiple division the body divides into a number of daughter individuals, with or without residual cytoplasmic masses of the parent body. In this process the nucleus may undergo either simultaneous multiple division, as in *Aggregata*, or more commonly, repeated binary fission, as in *Plasmodium* (Fig. 198) to produce large numbers of nuclei, each of which

becomes the center of a new individual. The number of daughter individuals often varies, not only among the different species, but also within one and the same species. Multiple division occurs commonly in the Foraminifera (Fig. 157), the Radiolaria (Fig. 167), a few Mastigophora such as *Trypanosoma lewisi* (Fig. 112), *T. cruzi*, and many Hypermastigina. It is very common among various groups of Sporozoa in which the trophozoite multiplies abundantly by this method.

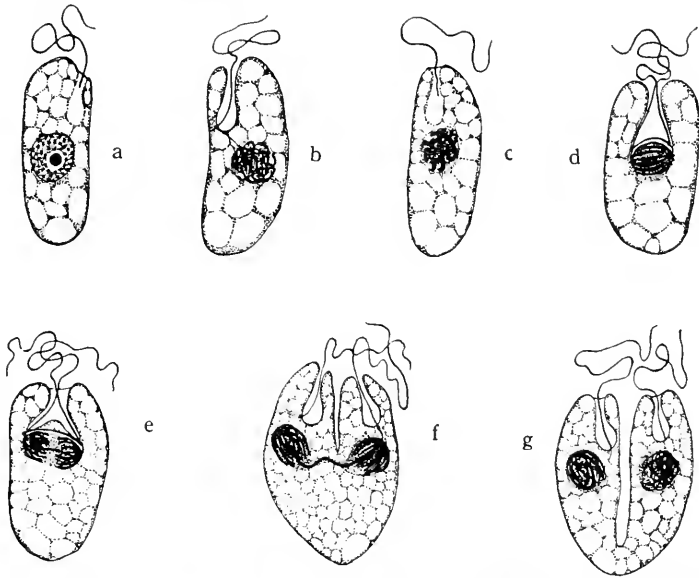


FIG. 64. Nuclear and cytosomic division in *Menoidium incurvum*. \times about 1400 (Hall). a, resting stage; b, c, prophase; d, equatorial plate; e, f, anaphase; g, telophase.

Budding. Multiplication by budding which occurs in the Protozoa is the formation of one or more smaller individuals from the parent organism. It is either exogenous or endogenous, depending upon the location of the developing buds or gemmules. Exogenous budding has been reported in *Acanthoecystis*, *Noctiluca* (Fig. 101), *Myxosporidia* (Fig. 65, b), astomous ciliates (Fig. 228), *Chonotricha*, *Suctorina* (Fig. 289, k), etc. Endogenous budding has been found in *Testacea*, *Gregarinida*, *Myxosporidia* (Figs. 212, e; 214, j), and other Sporozoa as well as *Suctorina* (Fig. 289, h). Collin observed a unique budding in *Tokophrya*

cyclopum in which the entire body, excepting the stalk and pellicle, transforms itself into a young ciliated bud which leaves sooner or later the parent pellicle as a swarmer.

Plasmotomy. Occasionally the multinucleate body of a protozoan divides into two or more small, multinucleate individuals,

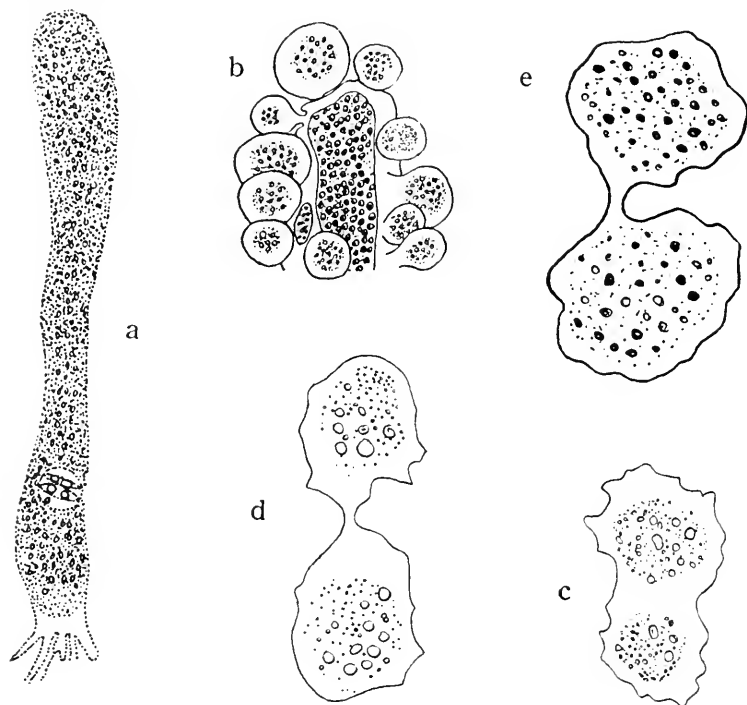


FIG. 65. a, b, budding in *Myxidium lieberkuhni*; c, d, plasmotomy in *Chloromyxum leydigi*; e, plasmotomy in *Sphaeromyxa balbianii*.

the cytosomic division taking place independently of nuclear division. This has been called plasmotomy by Doflein. It has been observed in the trophozoites of several coelozoic myxosporidians, such as *Chloromyxum leydigi* (Fig. 65), *Sphaeromyxa balbianii* (Fig. 65), etc. It occurs further in Mycetozoa (Fig. 135), Foraminifera and Protociliata.

Colony formation

When the division is repeated without a complete separation of the daughter individuals, a colonial form is produced. The

component individuals of a colony may either have protoplasmic connections among them or be grouped within a gelatinous envelope if completely separated. Or, in the case of loricate or stalked forms, these exoskeletal structures may become attached to one another. Although varied in appearance, the arrangement and relationship of the component individuals are constant, and this makes the basis for distinguishing the types of protozoan colonies, as follows:

Catenoid or linear colony. The daughter individuals are attached endwise, forming a chain of several individuals. It is of comparatively rare occurrence. Examples: Astomous ciliates such as *Radiophrya* (Fig. 228), *Protoradiophrya* (Fig. 228) and dinoflagellates such as *Ceratium*, *Haplozoon* (Fig. 103) and *Polykrikos* (Fig. 104).

Arboroid or dendritic colony. The individuals remain connected with one another in a tree-form. The attachment may be by means of the lorica, stalk or gelatinous secretions. It is a very common colony found in different groups. Examples: *Dinobryon* (Fig. 87), *Hyalobryon* (Fig. 87), etc. (connection by lorica); *Colacium* (Fig. 96), many *Peritricha* (Figs. 280; 282), etc. (by stalk); *Poteriodendron* (Fig. 109), *Stylobryon* (Fig. 119), etc. (by lorica and stalk); *Hydrurus* (Fig. 88), *Spongomonas* (Fig. 118), *Cladomonas* (Fig. 118) and *Anthophysa* (Fig. 119) (by gelatinous secretions).

Discoid colony. A small number of individuals are arranged in a single plane and grouped together by a gelatinous substance. Examples: *Cyclonexis* (Fig. 87), *Gonium* (Fig. 93), *Platydorina* (Fig. 94), *Protospongia* (Fig. 108), *Bicosoeca* (Fig. 109), etc.

Spheroid colony. The individuals are grouped in a spherical form. Usually enveloped by a distinct gelatinous mass, the component individuals may possess protoplasmic connections among them. Examples: *Uroglena* (Fig. 87, *c*), *Uroglenopsis* (Fig. 87, *d*), *Volvox* (Fig. 93), *Pandorina* (Fig. 94, *f*), *Eudorina* (Fig. 94, *h*), etc. Such forms as *Stephanoon* (Fig. 94, *a*) appear to be intermediate between this and the discoid type. The component cells of some spheroid colonies show a distinct differentiation into somatic and reproductive individuals, the latter apparently developing from certain somatic cells during the course of development.

The **gregaloid** colony, which is sometimes spoken of, is a loose

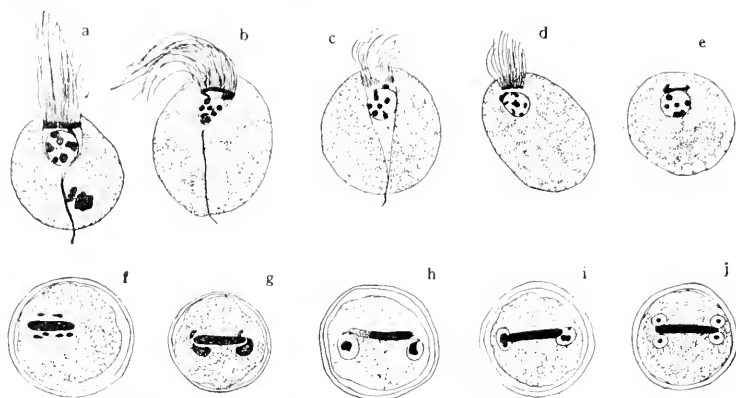


FIG. 66. Encystment of *Lophomonas blattarum*, $\times 1150$ (Kudo).

group of individuals of one species, usually of Sarcodina, which become attached to one another by means of pseudopodia in an irregular form.

Asexual reproduction

The Protozoa nourish themselves by certain methods, grow and multiply by the methods described in the preceding pages. This phase of the life-cycle of a protozoan is the vegetative stage or the **trophozoite**. The trophozoite repeats its asexual reproduction process under favorable circumstances. Generally speaking, the Sporozoa increase to a much greater number by schizogony and the trophozoites are called **schizonts**.

Under certain conditions, the trophozoite undergoes **encystment** (Fig. 66). Prior to encystment, the trophozoites cease to ingest, and extrude remains of food particles, resulting in somewhat smaller forms which are usually rounded and inactive. This is often called the **precystic stage**. The organism presently secretes substances which become solidified into the cyst wall and thus the cyst is formed. In this condition, the protozoan apparently is able to maintain its vitality for a certain length of time under unfavorable conditions. The causes of encystment are still the matter which many investigators are attempting to comprehend. It appears certain at least in some cases that the encystment is brought about by changes in temperature, desiccation, and chemical composition, amount of food material, accumulation of catabolic wastes, etc., in the medium in which the organisms

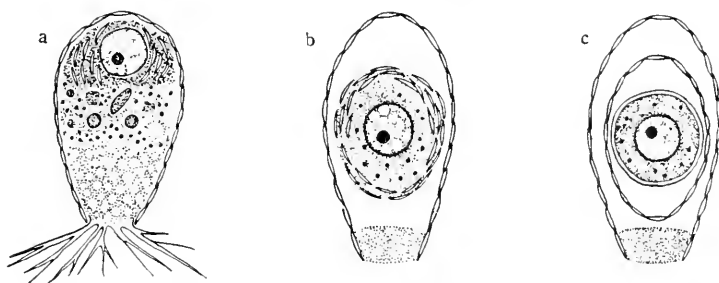


FIG. 67. Encystment of *Euglypha acanthophora*, $\times 320$ (Kühn).

live. In some cases, the organisms encyst temporarily in order to undergo nuclear reorganization and multiplication. Because of the latter condition and also of the failure in attempting to cause certain Protozoa to encyst under experimental conditions, some suppose that certain internal factors play as great a part as do the external conditions in the phenomenon of encystment. Ordinarily a single cyst wall seems to be sufficient to protect the protoplasm against unfavorable external conditions. In some cases there may be a double cyst wall, the inner one usually being more delicate. The cyst wall is generally composed of homogeneous substances, but it may contain calcareous scales as in *Euglypha* (Fig. 67). While chitin is the common material of which the cyst wall is composed, cellulose makes up the cyst envelope of numerous *Phytomastigina*.

The capacity of Protozoa to produce the cyst is probably one of the reasons why they are so widely distributed over the surface of the globe. The minute protozoan cysts are easily carried from place to place by wind, attached to soil particles, debris, etc., by the flowing water of rivers or the current in oceans or by insects, birds, other animals to which they become readily attached. When a cyst encounters a proper environment, the living protoplasmic contents excyst and the emerged organism once more return to its active trophic phase of existence.

In Sporozoa, no encystment occurs. Here at the end of active schizogony, sexual reproduction usually initiates the production of large numbers of the **spores** (Fig. 68).

Sexual reproduction and life-cycles

Besides reproducing by the asexual method, numerous Protozoa reproduce themselves in a manner comparable with the

sexual reproduction which occurs universally in the Metazoa. Various types of sexual reproduction have been reported in literature, of which a few will be considered here. The sexual fusion, which is a complete union of two gametes, has been reported from various groups, while the conjugation which is a

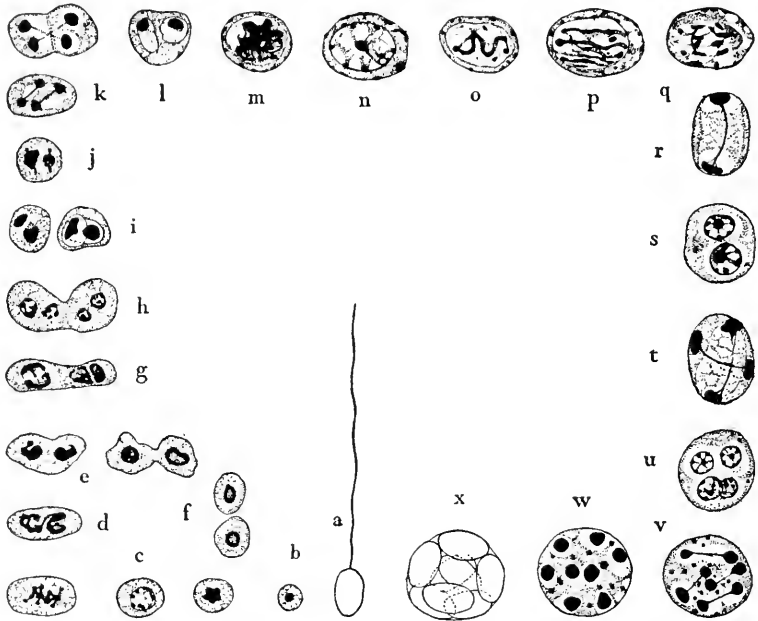


FIG. 68. Diagram illustrating the life-cycle of *Thelohania legeri* (Kudo). a, extrusion of the polar filament in gut of anopheline larva; b, emerged amoebula; c-f, schizogony in fat body; g-m, sporont-formation; n-x, spore-formation.

temporary union of two gametes for the purpose of exchanging the nuclear material, is found almost exclusively in the Ciliophora.

Sexual fusion. If the two gametes which take part in this process, are morphologically alike, they are called **isogametes** and the act the **isogamy**; but if unlike, **anisogametes**, and the act, **anisogamy**. The isogamy is typically represented by the flagellate *Copromonas subtilis* (Fig. 69), in which there occurs, according to Dobell, a complete nuclear and cytoplasmic fusion between two isogametes. Each nucleus, after casting off a portion

of its nuclear material, fuses with the other and the zygote thus formed, encysts. In *Stephanosphaera pluvialis* (Fig. 70), both asexual and sexual reproductions occur, according to Hieronymus. Each individual multiplies and develops into numerous biflagellate gametes, all of which are alike. Isogamy between two gametes results in formation of numerous zygotes which later develop into trophozoites.

Anisogamy has been observed in certain Foraminifera, Gregarinida (Lankesterella, Fig. 174; Schizocystis, Fig. 185), etc. It per-

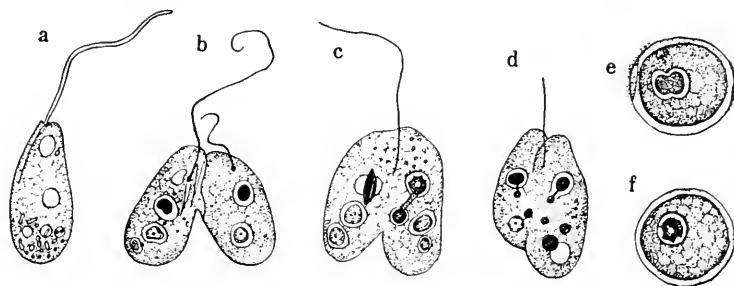


FIG. 69. Sexual fusion in *Copromonas subtilis*, $\times 1300$ (Dobell).

haps occurs in the Radiolaria also, although positive evidence has yet to be presented. Anisogamy seems to be more widely distributed. On the whole, the differences between the micro- and macro-gametes are comparable with those which exist between the spermatozoa and ova of the Metazoa. The microgametes are motile, relatively small and usually numerous, while the macrogametes are usually not motile, much more voluminous and fewer in number (Fig. 71). In *Chlamydomonas monadina* (Fig. 90), according to Goroschankin, the two gametes come in contact at the anterior end where the membranes become dissolved and the contents of the microgamete stream into the macrogamete. A new shell is then secreted around them. Later the shell becomes swollen and the organism multiplies into 2, 4, or 8 swimmers which in turn develop into the trophozoites. In *Pandorina morum* (Fig. 72), Pringsheim observed that each cell asexually develops into a young colony (a, b) or into anisogametes (c) which undergo sexual fusion (d-g) and encyst (h). The organism emerged from the cyst, develops into a young trophozoite (i-m). A similar life-cycle was found by Goebel in *Eudorina elegans* (Fig. 73).

Among the Sporozoa, anisogamy is of common occurrence. In

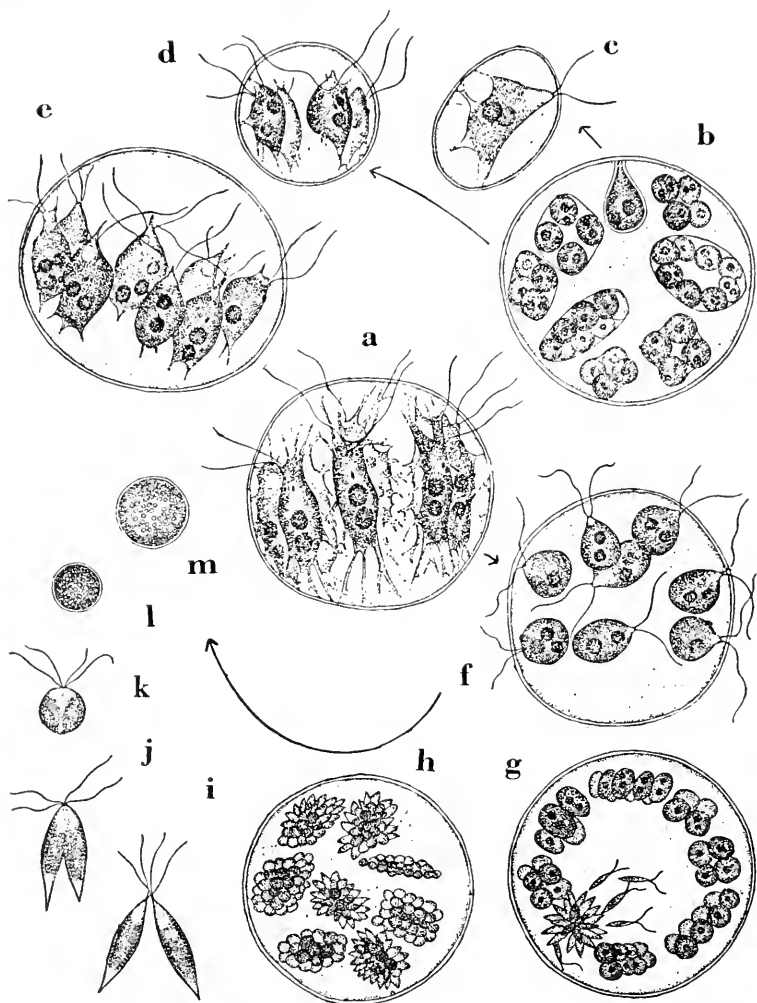


FIG. 70. The life-cycle of *Stephanosphaera pluvialis* (Hieronymus).
a-e, asexual reproduction; f-m, sexual reproduction.

Coccidia, the process was well studied in *Eimeria schubergi* (Fig. 188), *Aggregata eberthi* (Fig. 190), *Adelea ovata* (Fig. 194), etc., and the resulting products are the **oocyst** (zygote) in which the spores or sporozoites develop. Similarly in Haemosporidia such as *Plasmodium vivax* (Fig. 197), anisogamy results in the formation of the **ookinete** or motile zygote which gives rise to a large

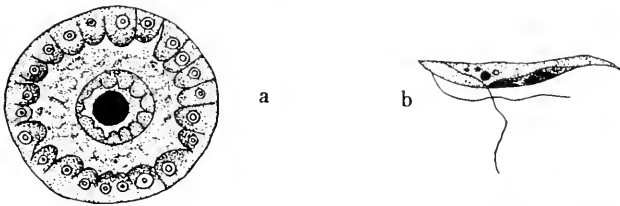


FIG. 71. a, macrogamete, and b, microgamete of *Volvox aureus*, $\times 1000$ (Klein).

number of sporozoites. Among Myxosporidia, a complete information as to how the initiation of sporogony is associated with sexual reproduction, is still lacking. Naville, however, states that

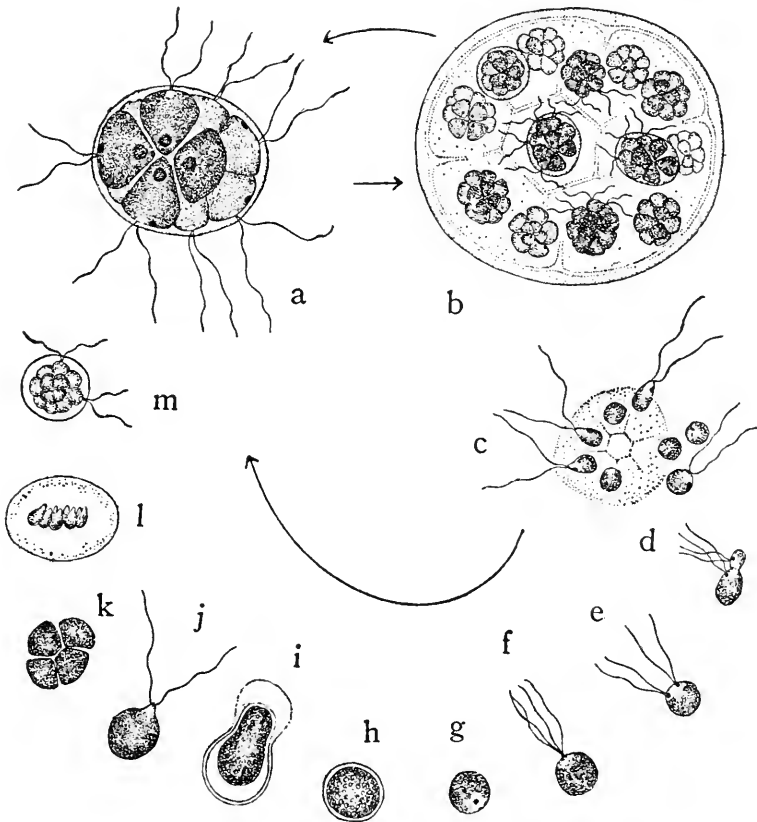


FIG. 72. The life-cycle of *Pandorina morum*, $\times 400$ (Pringsheim). a, b, asexual reproduction; c-m, sexual reproduction.

in the trophozoite of *Sphaeromyxa sabrazesi* (Fig. 210), micro- and macro-gametes develop, each with a haploid nucleus. Anisogamy, however, is peculiar in that the two nuclei remain independent. The microgametic nucleus divides once and the two nuclei remain as the vegetative nuclei of the pansporoblast, while the macrogamete nucleus multiplies repeatedly and develop into two spores. Anisogamy has been suggested to occur in some members of Amoebina, particularly in *Endamoeba blattae*. Mercier (1909) believed that in this amoeba there occurs anisogamy soon

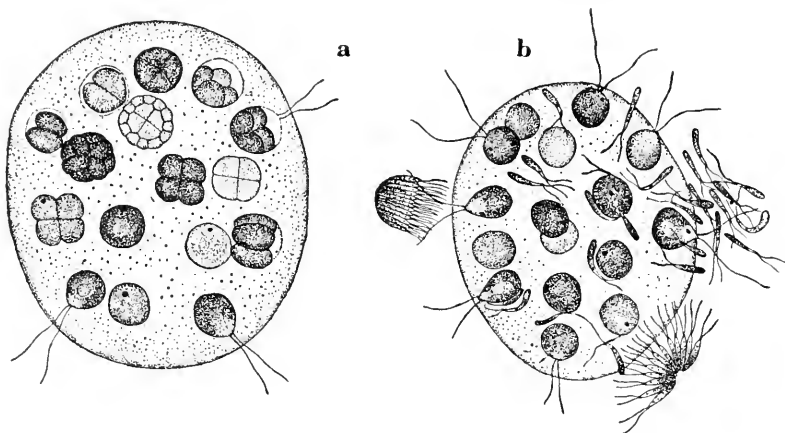


FIG. 73. The life-cycle of *Eudorina elegans* (Goebel). a, asexual reproduction; b, sexual reproduction, a female colony with clustered and isolated microgametes.

after excystment in the host's intestine, but this awaits confirmation. Cultural studies of various parasitic amoebae in recent years show no evidence of sexual reproduction in those forms.

Among the Ciliophora, the sexual fusion occurs only in Proto-ciliata (Fig. 225) and the conjugation described below is the usual method of sexual reproduction.

Conjugation. The conjugation is a temporary union of two individuals of one and the same species for the purpose of exchanging part of the nuclear material and occurs almost exclusively in the Euciliata and Suctoria. The two individuals which participate in this process may be either isogamous or anisogamous. In *Paramecium caudatum* (Fig. 74), two individuals come in contact on their oral surfaces. The micronucleus in each

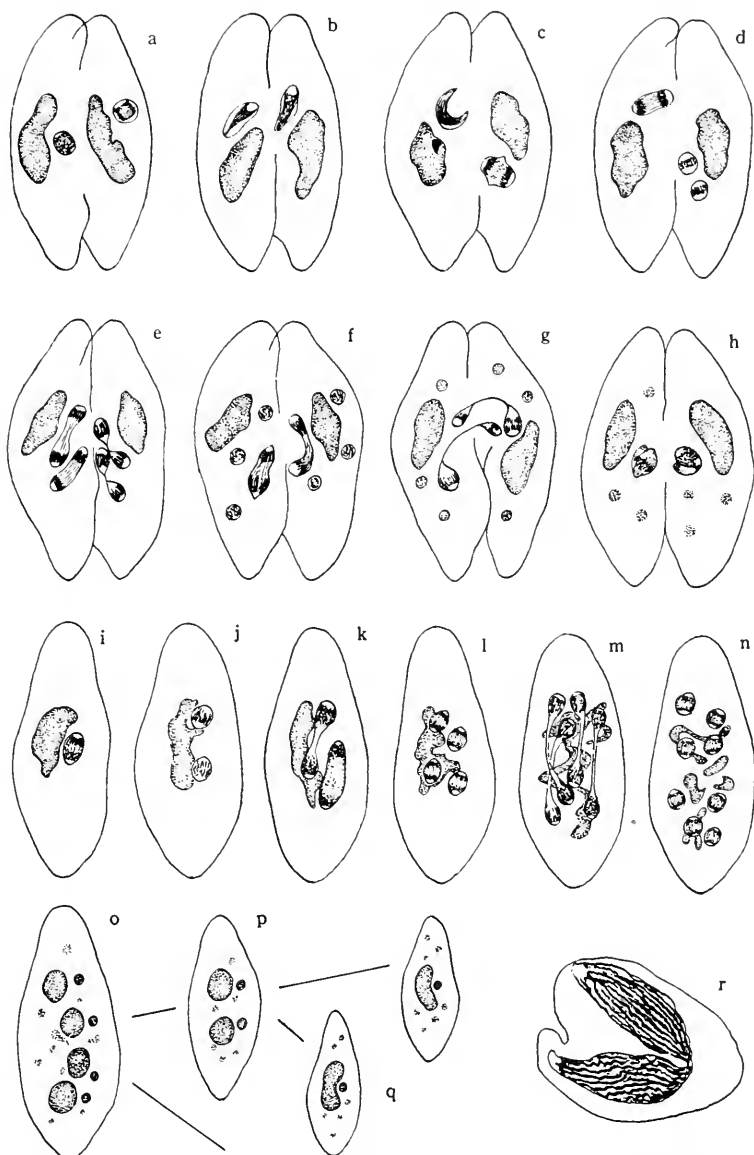


FIG. 74. Diagram illustrating the conjugation of *Paramecium caudatum*. a-q, \times about 130 (Calkins); r, \times 1200 (Dehorne).

conjugant divides twice (b-e), forming four micronuclei, three of which degenerate and do not take active part during further

changes ($f-h$). The remaining micronucleus divides once more, producing a wandering pronucleus and a stationary pronucleus (f, g). The wandering pronucleus in each of the conjugants enters the other individual and fuses with its stationary pronucleus (h, r). The two zygotes now separate from each other and become exconjugants. In each exconjugant, the synkaryon divides three times in succession ($i-m$) and produces eight nuclei (n), four of which remain as micronuclei, while the other four develop into new macronuclei (o). Cytosomic fission follows then, producing first, two individuals with four nuclei (p) and then, four small individuals, each containing a micronucleus and a macronucleus (a). According to Jennings, however, of the four smaller nuclei formed in the exconjugant indicated in Fig. 74, o , only one remains active, and the other three degenerate. This active nucleus divides prior to the cytosomic division so that in the next stage (p), there are two developing macronuclei and one micronucleus which divides once more before the second and last cytosomic division (q). During these changes the original macronucleus disintegrates, degenerates, and finally becomes absorbed in the cytoplasm.

When the ciliate possesses more than one micronucleus, the first division ordinarily occurs in all and the second may or may not take place in all, varying apparently even among individuals of the same species. In *Paramecium aurelia*, of the eight micronuclei formed by two fissions of the two original micronuclei, according to Woodruff, only one undergoes the third division to produce two pronuclei. This is the case with the majority, although more than one micronucleus may divide for the third time to produce several pronuclei, for example, two in *Euplotes patella*, *Stylonychia pustulata*; two to three in *Oxytricha fallax* and two to four in *Uroleptus mobilis*. This third division is always characterized by long extended nuclear membrane stretched between the division products.

Ordinarily the individuals which undergo conjugation appear to be morphologically similar to those that are engaged in the trophic activity, but in some species, the organism divides just prior to conjugation. According to Wichterman (1936), conjugation in *Nyctotherus cordiformis* (Fig. 75) takes place only among those which live in the tadpoles undergoing metamorphosis ($f-j$). The conjugants are said to be much smaller than the ordinary

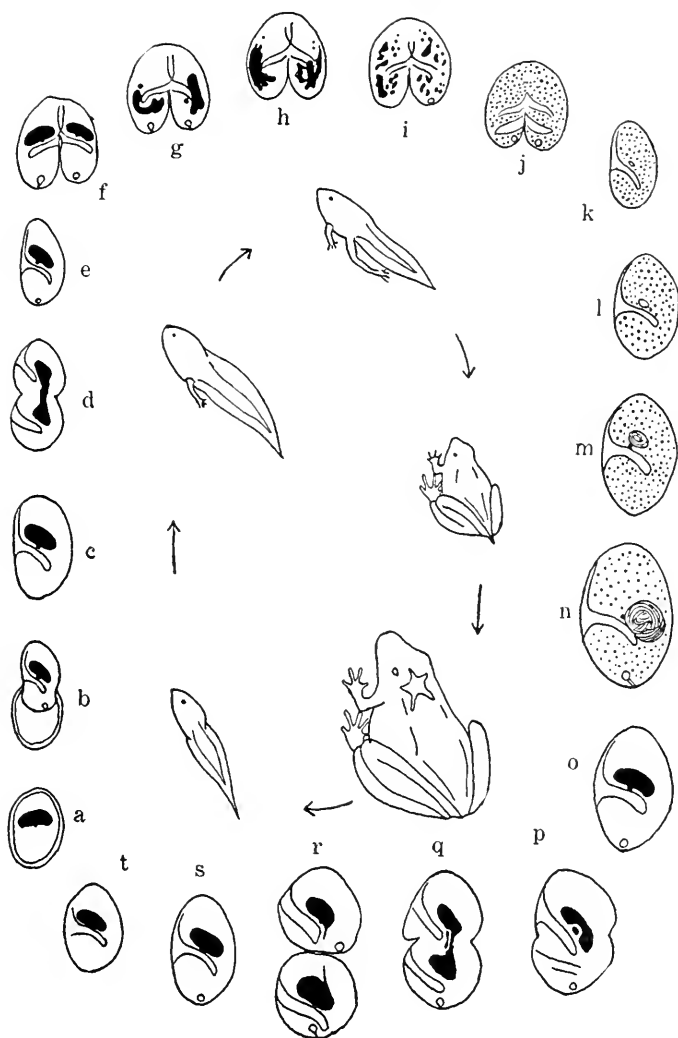


FIG. 75. The life-cycle of *Nyctotherus cordiformis* in *Hyla versicolor* (Wichterman). a, a cyst; b, excystment in tadpole; c, d, division is repeated until host metamorphoses; e, smaller pre-conjugant; f-j, conjugation; k, ex-conjugant; l, amphinucleus divides into 2 nuclei, one micronucleus and the other passes through the "spireme ball" stage before developing into a macronucleus; k-n, ex-conjugants found nearly exclusively in recently transformed host; o, mature trophozoite; p-s, binary fission stages; t, precystic stage.

trophozoites, because of the preconjugal fission (*d-e*). The micronuclear divisions are similar to those that have been described for *Paramecium caudatum* and finally two pronuclei are formed in each conjugant. Exchange and fusion of pronuclei follow. In each exconjugant, the synkaryon divides once to form the micronucleus and the macronuclear anlage (*k-l*) which develop into the "spireme ball" and finally into the macronucleus (*m-o*).

A sexual process which is somewhat intermediate between the sexual fusion and conjugation, is noted in several instances. According to Maupas' classical work on *Vorticella nebulifera*, the ordinary vegetative form divides twice, forming four small individuals, which become detached from one another and swim about independently. Presently each becomes attached to one side of a stalked individual. In it, the micronucleus divides three times and produces eight nuclei, of which seven degenerate; and the remaining nucleus divides once more. In the stalked form the micronucleus divides twice, forming four nuclei, of which three degenerate, the other dividing into two. During these changes the cytoplasm of the two conjugants fuse completely. The wandering nucleus of the smaller conjugant unites with the stationary nucleus of the larger conjugant, the other two pronuclei degenerating. The synkaryon divides several times to form a number of nuclei, from some of which macronuclei are differentiated and exconjugant undergoes multiplication.

Another example of this type has been observed by Noland (1927) in *Metopus es* (Fig. 76). According to Noland, the conjugants fuse at the anterior end (*a*), and the micronucleus in each individual divides in the same way as was observed in *Paramecium caudatum* (*b-e*). But the cytoplasm and both pronuclei of one conjugant pass into the other (*f*), leaving the degenerating macronucleus and a small amount of cytoplasm behind in the shrunken pellicle of the smaller conjugant which then separates from the other (*j*). In the larger exconjugant, two pronuclei fuse, and the other two degenerate and disappear (*g, h*). The synkaryon divides into two nuclei, one of which condenses into the micronucleus and the other grows into the macronucleus (*i-m*). This is followed by the loss of cilia and encystment.

What is the significance of conjugation? What are the conditions which bring about conjugation in the ciliates? These are

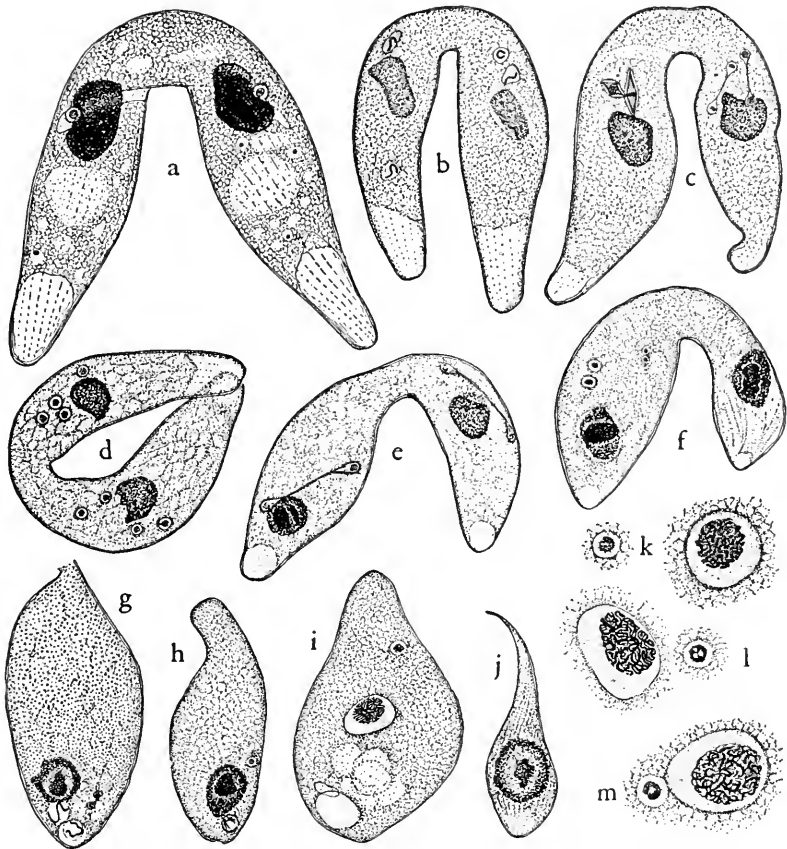


FIG. 76. Conjugation of *Metopus es* (Noland). a, early stage; b, first micronuclear division; c, d, second micronuclear division; e, third micronuclear division; f, migration of pronuclei from one conjugant into the other; g, large conjugant with two pronuclei ready to fuse; h, large conjugant with the synkaryon, degenerating pronuclei and macronucleus; i, large exconjugant with newly formed micronucleus and macronucleus, showing the degenerating old macronucleus; j, small exconjugant with degenerating macronucleus; k-m, development of two nuclei. a, $\times 290$; b-j, $\times 250$; k-m, $\times 590$.

but two of the many problems which numerous investigators attempted to solve since the appearance of the first comprehensive study of the phenomenon by Maupas in 1889. Woodruff's observation (1932) among others which showed that 5071 generations produced asexually from a single individual of *Paramecium*

aurelia between May 1, 1907 and May 1, 1915, did not manifest any decrease in vitality after eight years of asexual reproduction, demonstrates beyond doubt that the sexual reproduction in the form of conjugation is not necessary for the well-being of *Paramecium aurelia* under favorable environmental conditions. On the other hand, there is a large body of evidence to support the view expressed first by Maupas to the effect that the conjugation corrects an inherent tendency toward senescence under unfavorable conditions. Recently Sonneborn and Lynch (1932) demonstrated by using different clones of *P. aurelia* that the effects of conjugation are diverse and characteristic of different races: 1) the conjugation increases fission rate in some clones, decreases the rate in others; 2) it increases variation in some clones, but not in others; and 3) it increases mortality in some clones but not in others. Sonneborn (1937) continuing controlled observations on this ciliate, discovered that in certain races there are two classes of individuals with respect to sexual differentiation and that the members of different classes conjugate, while the members of each class do not. He further found that the individuals produced by binary fission from a single individual belong all to the sex reaction type to which the original individual belonged, and that in conjugation in which two sex reaction types participate, the four sets of progeny consist of the two types in chance combination, the ratio being identical with those for inheritance in higher organisms. Jennings (1938) found further four sex reaction types in *P. bursaria*, in which the type behavior toward conjugation was exactly like that of the two types found in *P. aurelia*.

Automixis. In certain Protozoa, the fusion occurs between two nuclei which originate in a single nucleus of an individual. This process has been called automixis by Hartmann, in contrast to the amphimixis (Weismann) which is the complete fusion of two nuclei originating in two individuals, as was discussed in the preceding pages. If the two nuclei which undergo a complete fusion are present in a single cell, the process is called **autogamy**, but, if they are in two different cells, then **paedogamy**. The autogamy is of common occurrence in the myxosporidian spores. The young sporoplasm contains two nuclei which fuse together prior to or during the process of germination in the alimentary canal of a specific host fish, as for example in *Sphaeromyxa sabrazesi* (Figs. 209; 210) and *Myxosoma catostomi* (Fig. 208). In

the Microsporidia, autogamy initiates the spore-formation at the end of schizogonic activity of individuals as in *Thelohania legeri* (Fig. 68).

Recently Diller (1936) observed in solitary *Paramecium aurelia* (Fig. 77), certain micronuclear changes similar to those which occur in conjugating individuals. The two micronuclei divide twice, forming eight nuclei, some of which divide for the third time, producing two functional and several degenerating nuclei. The two functional nuclei then fuse in the "preoral cone" and

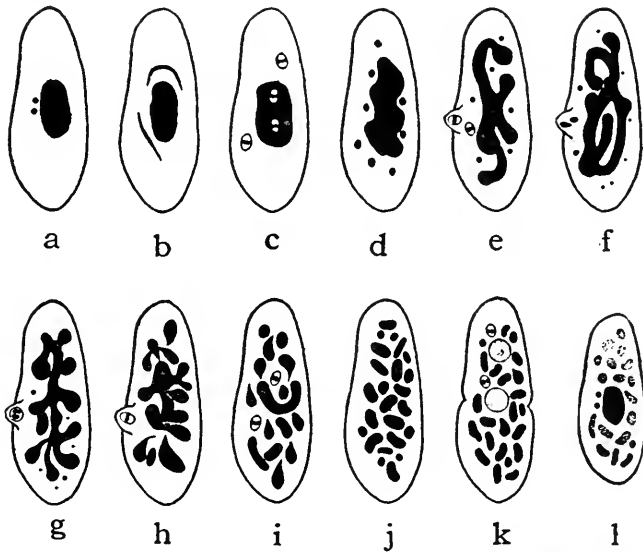


FIG. 77. Diagram illustrating autogamy in *Paramecium aurelia* (Diller). a, normal animal; b, first micronuclear division; c, second micronuclear division; d, individual with 8 micronuclei and a macronucleus preparing for skein formation; e, some micronuclei dividing for the third time, with two functional nuclei near 'preoral cone'; f, two gamete-nuclei formed by the third division in the cone; g, fusion of the nuclei, producing synkaryon; h, i, first and second division of synkaryon; j, with 4 nuclei, 2 becoming macronuclei and the other 2 remaining as micronuclei; k, macronuclei developing, micronuclei dividing; l, one of the daughter individuals produced by fission.

form the synkaryon which divides twice into four. The original macronucleus undergoes fragmentation and becomes absorbed in the cytoplasm. Of the four micronuclei, two transform into the new macronuclei and two remain as micronuclei, each dividing into two after the body divides into two. Diller is "inclined

to feel that if an animal does not happen to meet another individual in the same physiological condition as itself, its reorganizing 'urge' will be expressed by autogamy, as a substitute for conjugation."

The paedogamy occurs in at least two species of Myxosporidia, namely, *Leptotheca ohlmacheri* (Fig. 212) and *Unicapsula muscularis* (Fig. 213). The spores of these Myxosporidia contain two uninucleate sporoplasms which are independent at first, but prior to emergence from the spore, they undergo a complete fusion to metamorphose into a uninucleate amoebula. Perhaps the classical example of the paedogamy is that which was found by Hertwig (1898) in *Actinosphaerium eichhorni*. The organism encysts and the body divides into numerous uninucleate secondary cysts. Each secondary cyst divides into two and remains together within a common cyst-wall. In each the nucleus divides twice, and forms four nuclei, one of which remains functional, the remaining three degenerating. The paedogamy results in formation of a zygote in place of a secondary cyst. Bělař (1922) observed a similar process in *Actinophrys sol* (Fig. 78). The heliozoan withdraws its axopodia and divides into two uninucleate bodies which become surrounded by a common gelatinous envelope. Both nuclei divide twice and produce four nuclei, three of which degenerate. The two daughter cells, each with one haploid nucleus, undergo paedogamy and the resulting individual now contains a diploid nucleus.

Endomixis. Woodruff and Erdmann (1914) observed that in *Paramecium aurelia* (Fig. 79) at regular intervals of about 30 days, the old macronucleus breaks down and disappears, while each of the two micronuclei divide twice, forming eight nuclei. Of these, six disintegrate. At this point the organism divides into two, each daughter individual receiving one micronucleus. This nucleus soon divides twice into four, two of which develop into macronuclei, and the other two divide again. Here the organisms divide once more by binary fission, each bearing one macronucleus and two micronuclei. This process which is "a complete periodic nuclear reorganization without cell fusion in a pedigreed race of *Paramecium*" was called by the two authors endomixis. In the case of *P. caudatum*, they found endomixis occurs at intervals of about 60 days. Sonneborn (1937) succeeded in inducing endomixis in certain stocks of *P. aurelia* by placing

small mass cultures containing surplus animals from isolation lines at 31°C. for 1–2 days. Endomixis has since been observed more often in encysted stage of *Spathidium spathula*, *Uroleptus mobilis*, *Euplotes longipes*, *Didinium nasutum*, etc. As to its significance, the statement made for conjugation appears also to hold true.

In *Paramecium aurelia*, Diller (1936) found simple fragmenta-

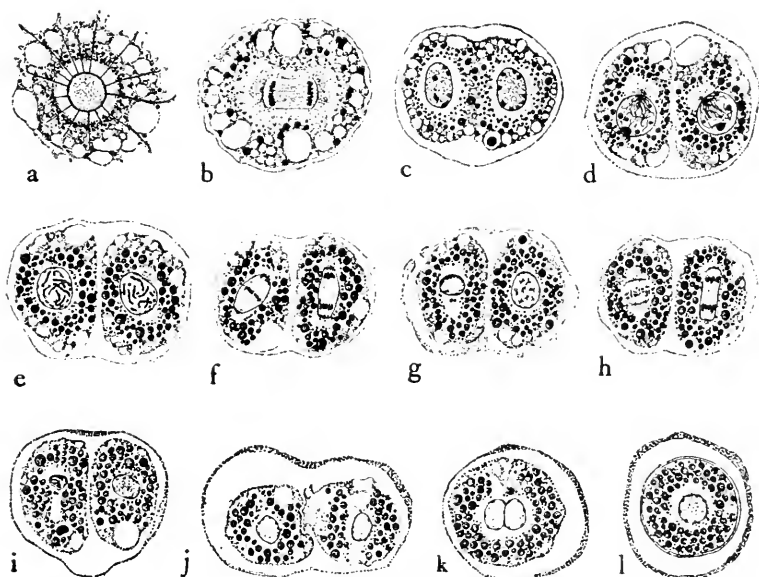


FIG. 78. Paedogamy in *Actinophrys sol*, $\times 460$ (Bělař). a, withdrawal of axopodia; b, c, division into two uninucleate bodies, surrounded by a common gelatinous envelope; d–f, the first reduction division; g–i, the second reduction division; j–l, synkaryon formation.

tion of the macronucleus which was not correlated with any special micronuclear activity and which could not be stages in conjugation or autogamy. Diller suggests that if conjugation or autogamy is to create a new nuclear complex, as is generally held, it is conceivable that somewhat the same result might be achieved by 'purification act' (through fragmentation) on the part of the macronucleus itself, without involving micronuclei. He coined the term 'hemixis' to include these reorganizations.

Meiosis. In the foregoing sections, references have been made

to the divisions which the nuclei undergo prior to sexual fusion or conjugation. In all Metazoa, during the development of the gametes, the gametocytes undergo reduction division or meiosis, by which the number of chromosomes is halved; that is to say, each fully mature gamete possesses half number (haploid) of chromosomes typical to the species (diploid). In the zygote, the

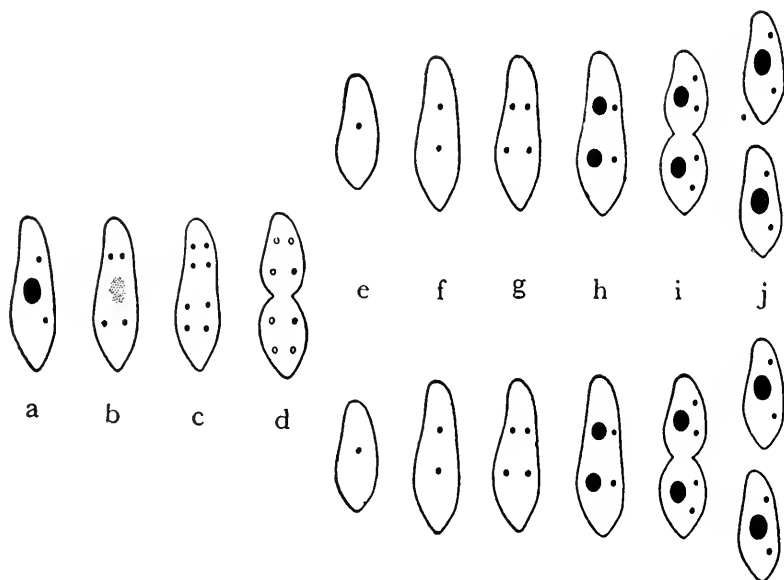


FIG. 79. Diagram showing the endomixis in *Paramecium aurelia* (Woodruff). a, normal individual; b, degeneration of macronucleus and first micronuclear division; c, second micronuclear division; d, degeneration of 6 micronuclei; e, cell division; f, g, first and second reconstruction micronuclear division; h, transformation of 2 micronuclei into macronuclei; i, micronuclear and cell division; j, typical nuclear condition is restored.

diploid number is reestablished. In the Protozoa in which sexual reproduction occurs during their life-cycle, meiosis presumably takes place to maintain the constancy of chromosome-number, but the process is understood only in a small number of species.

In conjugation, the meiosis seems to take place in the second micronuclear division, although in some, for example, *Oxytricha fallax*, according to Gregory, the actual reduction occurs during the first division. Prandtl (1906) was the first to note a reduction

in number of chromosomes in the Protozoa. In conjugating *Didinium nasutum*, he observed 16 chromosomes in each of the daughter micronuclei during the first division, but only 8 in the second division. Since that time, the fact that meiosis occurs during the second micronuclear division has been observed in *Chilodonella uncinata* (Enrique; MacDougall), *Carchesium poly-pinum* (Popoff), *Uroleptus halseyi* (Calkins), etc. (see the ciliates in the list on p. 135). In various species of *Paramecium* and many other forms, the number of chromosomes appears to be too great to allow a precise counting, but it is generally agreed that here probably reduction in the number also takes place.

Information on the meiosis involved in the complete fusion of gametes is even more scanty and fragmentary. In *Monocystis rostrata*, a parasite of the earthworm, Mulsow noticed that the nuclei of two gametocytes which encyst together, multiply by mitosis in which eight chromosomes are constantly present, but in the last division in gamete formation, each daughter nucleus receives only 4 chromosomes. In another species of *Monocystis*, Calkins and Bowling (1926) observed that the diploid number of chromosomes was 10 and that haploid condition is established in the last gametic division, thus confirming Mulsow's finding.

In the paedogamy of *Actinophrys sol*, Bělař found 44 chromosomes in the first nuclear division, but after two meiotic divisions, the remaining functional nucleus contains only 22 chromosomes so that when paedogamy is completed the diploid number is restored. On the other hand, in the coccidian *Aggregata eberthi* (Fig. 190), according to Dobell and Jameson, Bělař, and Naville, and in the gregarine *Diplocystis schneideri*, according to Jameson, there is no reduction in the number of chromosomes during the gamete-formation, but the first zygotic division is meiotic, 12 to 6 and 6 to 3, respectively. A similar reduction in chromosome (12 to 6) takes place also in the gregarine *Zygosoma globosum*, according to Noble's recent study (1938). Thus it appears in these cases that the zygote or oocyst is the only stage in which diploid nucleus occurs, while the nuclei in the stages in the remainder of the life-cycle are haploid.

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Variation and heredity

IT is generally recognized that individuals of a species of organism show a greater or less morphological variation. Protozoa are no exceptions. Various Protozoa manifest a wide variation in a limited or in widely separated localities so that different groups of the same species are spoken of as races, varieties, etc. It is well-known that dinoflagellates show a great morphological variation in different localities. Schröder (1914) showed that there were at least nine varieties of *Ceratium hirundinella* (Fig. 80) occurring in various waters of Europe, and List found that the organisms living in shallow ponds showed a marked morphological difference from those living in deep ponds. *Cyphoderia ampulla* is said to vary in size among those inhabiting the same deep lakes, namely, individuals from deep water may reach 200μ in length, while those from the surface water measure only about 100μ long.

In Foraminifera, the shell varies in thickness even in one and the same species, depending upon the part of the ocean in which they live. Thus the forms which live floating in surface water have a much thinner shell than those which dwell on the bottom of the ocean. For example, according to Rhumbler, *Orbulina universa* inhabiting surface water has a very thin shell, $1.28-18\mu$ thick, while individuals living on the bottom may show a thick shell, up to 24μ in thickness. According to Uyemura, *Amoeba* sp., occurring in the thermal waters of Japan, showed a distinct dimensional difference in different springs; namely, it varied from $10-40\mu$ in diameter in sulphurous water, and from $45-80\mu$ in ferrous water; in both types of water the amoebae were larger at $36-40^{\circ}\text{C}$. than at 51°C . Such differences in morphological characteristics appear to be influenced by environmental conditions, and will continue to exist under those conditions, but when the organisms are subjected to a similar environment the differences disappear, as has been demonstrated by many observers.

Evidences obtained by various investigators point to a general conclusion that when environmental influences are brought upon

a protozoan at the time of nuclear reorganization either by division, conjugation, or by endomixis, they may bring about long-lasting modifications (Jollos) or mutations. In Popoff's experiment with *Stentor* and in Chatton's with *Glaucoma*, both

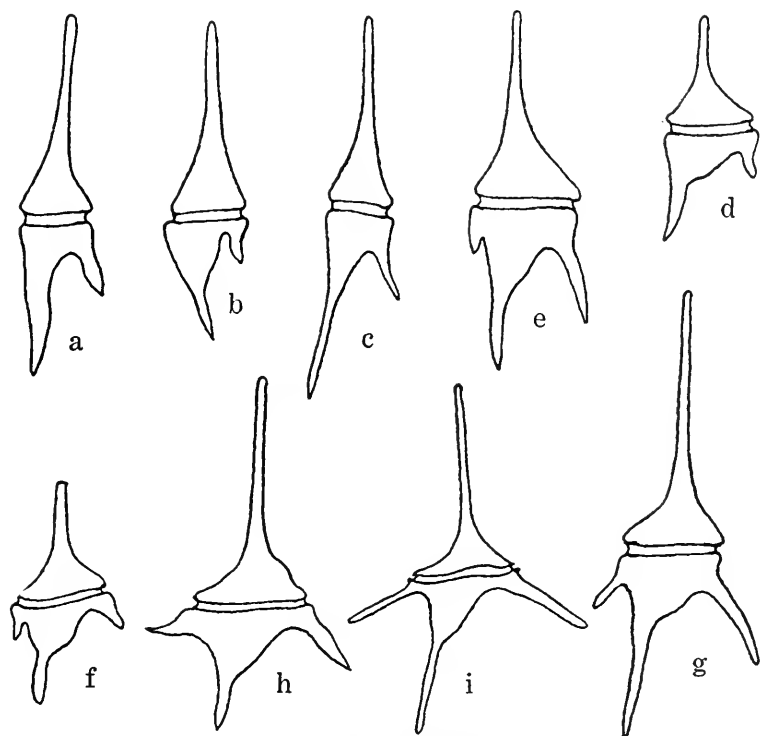


FIG. 80. Varieties of *Ceratium hirundinella* from various European waters (Schröder). a, *furcoides*-type (130–300 μ by 30–45 μ); b, *brachyceroides*-type (130–145 μ by 30–45 μ); c, *silesiacum*-type (148–280 μ by 28–34 μ); d, *carinthiacum*-type (120–145 μ by 45–60 μ); e, *gracile*-type (140–200 μ by 60–75 μ); f, *austriacum*-type (120–160 μ by 45–60 μ); g, *robustum*-type (270–310 μ by 45–55 μ); h, *scotticum*-type (160–210 μ by 50–60 μ); i, *piburgense*-type (180–260 μ by 50–60 μ).

conducted during the asexual division, long-lasting modifications have appeared in the experimental animals. Calkins (1924) observed a double-type *Uroleptus mobilis* which was formed by a complete fusion of two conjugants. This abnormal animal divided 367 times, living for 405 days, but reverted into normal forms

without reversion to a double form. It is probable that the organism showed a long-lasting modification, but there was no constitutional change in the organization of the animal. Jollos (1913-1934) observed that *Paramecium*, when subjected to various environmental influences, such as high temperature, arsenic acid, etc., showed variations which were gradually lost, although lasting through one or more periods of conjugation and endomixis, and that if the organisms were subjected to environmental changes during the late phase of conjugation, certain

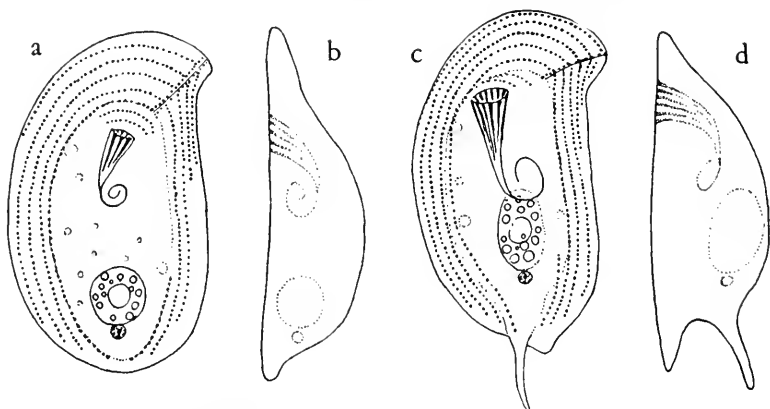


FIG. 81. *Chilodonella uncinata* (MacDougall). a, b, ventral and side view of normal individual; c, d, ventral and side view of the tailed mutant.

individuals, if not all, become permanently changed. Possibly here one sees that the reorganizing nuclear material has been affected in such a way that the hereditary constitution or genotype has become altered.

MacDougall subjected *Chilodonella uncinata* to ultraviolet rays and produced many changes which were placed in three groups: 1) abnormalities which caused the death of the organism; 2) temporary variations which disappeared by the third generation; and 3) variations which were transferred unchanged through successive generations, hence considered as mutations. The mutants were triploid, tetraploid, and tailed diploid forms (Fig. 81), which bred true for a variable length of time in pure-line cultures, either being lost or dying off finally. The tailed form differed from the normal form in the body shape, the number of

ciliary rows, with three contractile vacuoles, and mode of movement, but during conjugation showed the diploid number of chromosomes as in the normal form. The tailed form remained true and underwent 20 conjugations during ten months.

The first comprehensive study dealing with the variation in size with respect to inheritance in the uniparental reproduction of Protozoa was done by Jennings (1909). From a "wild" lot of *Paramecium*, Jennings isolated eight races with the relative mean lengths of 206, 200, 194, 176, 142, 125, 100, and 45μ which were inherited in each race. It was found further that within each clone derived from a single parent the size of different component individuals varies extremely, which is attributable to growth, amount of food and other environmental conditions, any one of which may give rise to progeny of the same mean size. Jennings thus showed that selection within the pure race has no effect on the size and that differences brought about merely by environment are not inherited.

Jennings (1916) also studied the inheritance of size and number of spines, dimensions of tests, diameter of mouth and size and number of teeth of the testacean *Diffugia corona*, and found that "a population consists of many hereditarily diverse stocks, and a single stock, derived from a single progenitor, gradually differentiates into such hereditarily diverse stocks, so that by selection marked results are produced." Root (1918) with *Centropyxis aculeata*, Hegner (1919) with *Arcella dentata*, and Reynolds (1923) with *A. polypora*, obtained similar results. Jennings (1937) carried on his study on the inheritance of teeth in *Diffugia corona* further in normal reproduction and by altering the mouth and teeth of the parent by operation, and observed that operated normal mouth or teeth were restored in three to four generations and that three factors appeared to determine the character and number of teeth: namely, the size of the mouth, the number and arrangement of the teeth in the parent, and "something in the constitution of the clone (its genotype) which tends toward the production of a mouth of a certain size, with teeth of a certain form, arrangement and number."

In the case of biparental inheritance, two nuclei of two different individuals participate to produce new combinations which would naturally bring about a greater variation among the offspring. For example, if two individuals from a single clone of a

ciliate, conjugate and the exconjugants are allowed to reproduce by fission, the descendants will show a greater variation among them with respect to the dimensions, fission-rate, etc. Thus several new biotypes may appear. If conjugation takes place between individuals of different clones and the descendants of

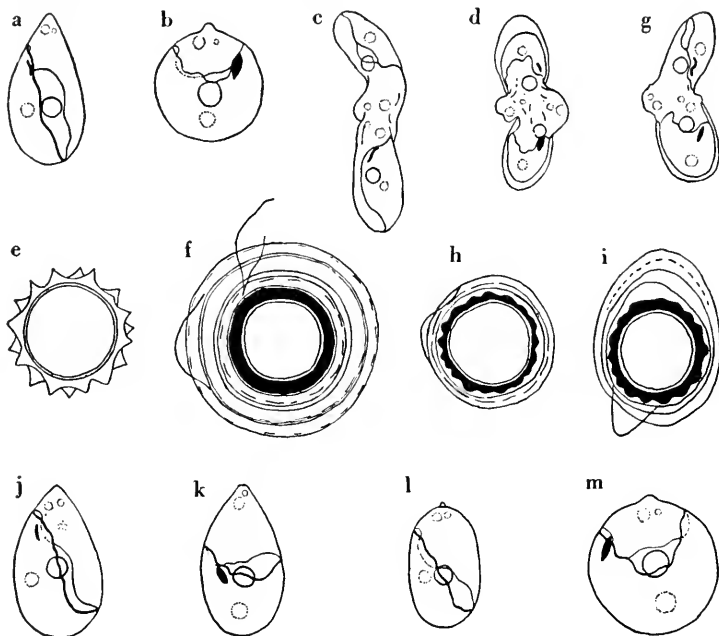


FIG. 82. Hybridization in *Chlamydomonas* (Paseher). a, vegetative individual of *Chlamydomonas* I; b, that of II; c, sexual fusion of two gametes of I; d, that of two gametes of II; e, homozygote of I; f, homozygote of II; g, sexual fusion of a gamete of I with a gamete of II; h, i, heterozygotes between I and II; j-m, four types of individuals arising from a heterozygote in culture.

this pair in turn conjugate and multiply by fission, the progeny will show conditions comparable to those which one sees in Mendelian inheritance in higher animals. In nature and in mass culture, it is supposed that this process is taking place continuously.

Since various species of Protozoa commonly co-inhabit small confines of water in nature, it is probable that hybridization between varieties or species may occur. Information on hand on

experimental hybridization of Protozoa is however very meager. Pascher (1916) succeeded in producing a small number of hybrid zygotes between two species of *Chlamydomonas* (Fig. 82). The two possessed the following characteristics. SPECIES I: pyriform; without a membrane-papilla; with a delicate membrane; flagella about twice the body length; chromatophore and pyrenoid lateral; nucleus central; stigma a narrow streak in the anterior third; with 2 contractile vacuoles (*a*); division into 4 zoospores; gametes up to 8, narrowed without membrane; zygote deeply sculptured and without spreading envelope (*e*). SPECIES II: spherical; with a distinct membrane and a membrane-papilla; chromatophore and pyrenoid posterior; nucleus central; stigma more anterior and fusiform; flagella short (*b*); division into 4 zoospores; gametes ellipsoid, ends rounded; zygote with a smooth but spreading envelope; with discarded gamete membrane (*f*). The hybrid-zygotes were morphologically intermediate (*h*, *i*) between the two parent zygotes. Thirteen zygotes were reared and in five cultures the offspring were either species I or II, two of each four zoospores being similar to those of I and the other two similar to those of II. In the eight cultures, each zygote developed into four different zoospores. Pascher described these four zoospores (*j-m*), which tended to indicate that for each of several pairs of characters, two zoospores possessed that of I and the other two that of II and that hybridization brought together two diverse sets of determiners in the heterozygote, which became segregated into four new sets of determiners, because of reduction during the formation of zoospores. These zoospores were however less active and abnormal so that they finally died in the culture without further development. Strehlow (1929) attempted to produce hybrids from three combinations of species of *Chlamydomonas*, succeeding in only one. Heterozygotes were obtained from the "positive" strain of *C. paradoxa* and the "negative" strain of *C. botryodes* (Fig. 83). Germination of the zygotes was however not observed.

Hybridization between different varieties or different species of the same genus of ciliates, was either unsuccessful or not genetically studied until quite recently. By using different clones of *Paramecium aurelia* which differed in fission rate, viability, and body length, Sonneborn and Lynch succeeded in following through three or four sexual generations and observed: "Groups

of hybrid clones obtained by crossing diverse clones manifested, on the average, characteristics intermediate between those of the parent clones or intermediate between those of the two groups of clones obtained by inbreeding the parent clones. Hybrid clones are of two types differing in the origin of their cytoplasm and

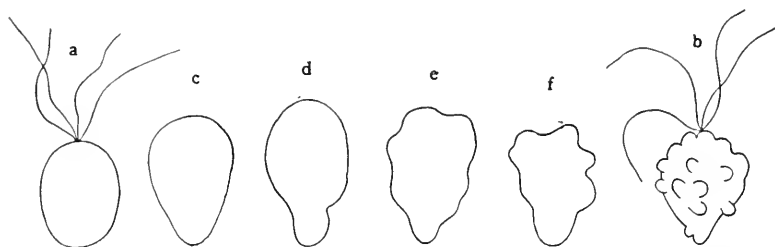


FIG. S3. Hybridization of *Chlamydomonas* (Strehlow). a, *C. paradoxa*; b, *C. botryodes*; c-f, heterozygotes between them.

macronuclear fragments; one type derives these from one parent clone, the other type from the other parent clone entering into the cross. One hybrid clone of each type arises from each pair of hybrid exconjugants. Sets of each of the two types of hybrid clones, as well as groups including both types of sets, were intermediate in characteristics. When hybrids of either type of cytoplasmic descent were inbred, the resulting F₂ generation included some clones resembling one parent, some clones resembling the other parent, and some clones with intermediate characteristics. When such F₂ segregates were further inbred, the resulting F₃ generation showed that some F₂ segregates were pure and others still mixed in genetic constitution."

Sonneborn and Lynch point out further that "there is no longer ground for doubting that the nucleus carries the determiners of hereditary characters, and there is considerable evidence that the nucleus carries these determiners arranged in separable pairs like the chromosomes or genes of higher organisms. If the cytology of the chromosomes in *Paramecium* were better known, the exact strength of the latter point could be more precisely estimated. For *P. aurelia*, Hertwig (1889) described a small number of chromosomes (8-10) undergoing conventional reduction during conjugation; but other investigators of this species have not hazarded chromosome counts and have given the impression that little progress in *Paramecium* chromosome cytology can be ex-

pected with present methods. Unless further progress can be made in cytological studies, the burden of attack must fall all the more heavily on purely genetic methods. On the basis of genetic work alone, we are led to conclude that the usual Mendelian situation, modified by certain details peculiar to the organism, probably exists in *Paramecium*. In agreement with Pascher, we find the fundamental patterns of protozoan and metazoan genetics to be very nearly the same."

De Garis produced monsters in *P. caudatum* by exposing dividing individuals either to low temperature or cyanide vapor, which were L-shaped and one or both components divided usually on the second or third day, producing free individuals. The genetic constitution of progeny was not altered by the experience of monster formation. By bringing about conjugation between monsters and free individuals which differed in fission rate and body length, De Garis produced hereditary diverse races from the two lines. On the other hand, the conjugation between *P. aurelia* and double monster of *P. caudatum* was found to have lethal effects on both ciliates, as the former species degenerated ("cloudy swelling") and died on the second or third day after conjugation, while the latter species manifested hyaline degeneration and died on the second to twelfth day after conjugation.

The discovery of sex reaction types in *Paramecium aurelia* and *P. bursaria*, as was stated in the last chapter, and further researches along this line, will, it is hoped, throw a clearer light on various genetical problems in Protozoa.

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CHAPTER 7

Phylum **Protozoa** Goldfuss

THE Protozoa are divided into two subphyla as follows:

Locomotor organellae, pseudopodia or flagella, or lacking (in Sporozoa); nucleus of one kind.....Subphylum 1 Plasmodroma
Locomotor organellae, cilia or cirri; nuclei of two kinds.....
.....Subphylum 2 Ciliophora (p. 481)

Subphylum 1 **Plasmodroma** Doflein

Class 1 **Mastigophora** Diesing

The Mastigophora includes those Protozoa which possess one to several flagella. Aside from this common characteristic, this class makes a very heterogeneous assemblage and seems to prevent a sharp distinction between the Protozoa and the Protophyta, as it includes Phytomastigina which are often dealt with by botanists.

In the majority of Mastigophora, each individual possesses 1-4 flagella during the vegetative stage, although species of Polymastigina may possess up to 8 or more flagella and of Hypermastigina a greater number of flagella. The palmella stage (Fig. 84) is common among the Phytomastigina and, unlike the encysted stage, the organism is capable in this stage not only of metabolic activity and growth, but also of reproduction. In this respect, this group shows also a close relationship to algae.

All three types of nutrition, carried on separately or in combination, are to be found among the members of Mastigophora. In holophytic forms, the chlorophyll is contained in the chromatophores which are of various forms among different species and which differ in colors, from green to red. The difference in color appears to be due to the pigments which envelop the chlorophyll body (p. 79). Many forms adapt their mode of nutrition to changed environmental conditions, for instance, from holophytic to saprozoic in the absence of the sunlight. Holozoic, saprozoic and holophytic nutrition are said to be combined in such a form as *Ochromonas*. In association with chromatophores, there occurs a refractile granule or body, the pyrenoid, which is connected

with starch-formation. Reserve food substances are starch, oil, etc. (p. 94-95).

In less complicated forms, the body is naked except for a slight cortical differentiation of the ectoplasm to delimit the body surface and is capable of forming pseudopodia. In others, there occurs a thin plastic pellicle produced by the cytoplasm, which covers the body surface closely. In still others, the body form is constant, being encased in a shell, test, or lorica, which is composed of chitin, pseudochitin, or cellulose. Not infrequently a gelatinous secretion envelops the body. In three families of *Protomonadina* there is a collar-like structure located at the anterior end, through which the flagellum protrudes.

The great majority of *Mastigophora* possess a single nucleus, and only a few are multinucleated. The nucleus is vesicular and contains a conspicuous endosome. Contractile vacuoles are always present in the forms inhabiting fresh water. In simple forms, the contents of the vacuoles are discharged directly through the body surface to the exterior; in others there are several contractile vacuoles arranged around a reservoir which opens to the exterior through the so-called cytopharynx. In the *Dinoflagellata*, there are apparently no contractile vacuoles, but non-contractile pusules (p. 217) occur in some forms. In chromatophore-bearing forms, there occurs usually a stigma which is located near the base of the flagellum and seems to be the center of phototactic activity of the organism which possesses it (p. 79).

Asexual reproduction is, as a rule, by longitudinal fission, but in some forms multiple fission also takes place under certain circumstances, and in others budding may take place. Colony-formation (p. 140), due to incomplete separation of daughter individuals, is widely found among this group. Sexual reproduction has been reported in a number of species.

The *Mastigophora* are free-living or parasitic. The free-living forms are found in fresh and salt waters of every description; many are free-swimming, others creep over the surface of submerged objects, and still others are sessile. Together with algae, the *Mastigophora* compose a major portion of plankton life which makes the foundation for the existence of all higher aquatic organisms. The parasitic forms are ecto- or endo-parasitic, and the latter inhabit either the digestive tract or the circulatory system of the host animal. *Trypanosoma*, a representative genus

of the latter group, includes important disease-causing parasites of man and of domestic animals.

The Mastigophora are divided into two subclasses as follows:
 With chromatophores. Subclass 1 Phytomastigina
 Without chromatophores. Subclass 2 Zoomastigina (p. 235)

Subclass 1 **Phytomastigina** Doflein

The Phytomastigina possess the chromatophores and their usual method of nutrition is holophytic, though some are holozoic, saprozoic or mixotrophic; the majority are conspicuously colored; some that lack chromatophores are included in this group, since their structure and development resemble closely those of typical Phytomastigina.

1-4 flagella, either directed anteriorly or trailing

Chromatophores yellow, brown or orange

Anabolic products fat, leucosin. Order 1 Chrysomonadina

Anabolic products starch or similar carbohydrates.
 Order 2 Cryptomonadina (p. 184)

Chromatophores green

Simple contractile vacuole, anabolic products starch and oil. .
 Order 3 Phytomonadina (p. 188)

Contractile vacuole complex

Anabolic products paramylon. Order 4 Euglenoidina (p. 203)

Anabolic products oil. Order 5 Chloromonadina (p. 213)

2 flagella, one of which transverse. Order 6 Dinoflagellata (p. 216)

Order 1 **Chrysomonadina** Stein

The chrysomonads are minute organisms and are plastic, since the majority lack a definite cell-wall. Chromatophores are yellow to brown (rarely green or bluish) and usually discoid, though sometimes reticulated, in form. Metabolic products are refractile bodies, known collectively as leucosin (probably carbohydrates) and fats. Starches have not been found in them. 1-2 flagella are inserted at or near the anterior end of body where a stigma is present.

Many chrysomonads are able to form pseudopodia for obtaining food materials which vary among different species. Nutrition, though chiefly holophytic, is sometimes holozoic or saprozoic. Contractile vacuoles are invariably found in freshwater forms, and are ordinarily of simple structure, although a complicated system seems to be found in some.

Under conditions not fully understood, the Chrysomonadina lose their flagella and undergo division with development of mucilaginous envelope and thus transform themselves often into large bodies known as the palmella phase and undertake metabolic activities as well as multiplication (Fig. 84). Asexual reproduction is, as a rule, by longitudinal division during either the motile or the palmella stage. Incomplete separation of the daughter individuals followed by repeated fission, results in numerous colonial forms mentioned elsewhere (p. 141). Some

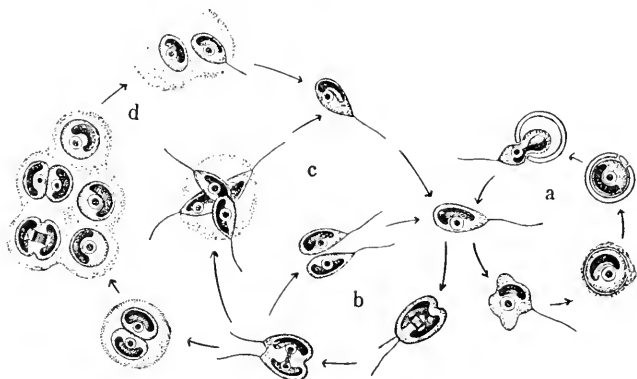


FIG. 84. The life-cycle of *Chromulina*, \times about 200 (Kühn). a, encystment; b, fission; c, colony-formation; d, palmella-formation.

resemble higher algae very closely. Sexual reproduction is entirely unknown in this group. Encystment occurs commonly; in this the flagellum is lost and the cyst is enveloped by a silicious wall possessing an opening with a plug.

The chrysomonads inhabit both fresh and salt waters, often occurring abundantly in plankton.

Motile stage dominant. Suborder 1 *Euchrysomonadina*

Palmella stage dominant

Sarcodina-like; flagellate stage unknown.

. Suborder 2 *Rhizochrysidina* (p. 181)

Palmella phase dominant. Suborder 3 *Chrysocapsina* (p. 182)

Suborder 1 ***Euchrysomonadina*** Pascher

With or without simple shell

One flagellum. Family 1 *Chromulinidae* (p. 175)

2 flagella

Flagella equally long. Family 2 *Syncryptidae* (p. 177)

Flagella unequally long. Family 3 *Ochromonadidae* (p. 179)

With calcareous or silicious shell

Bearing calcareous discs and rods. . Family 4 Coccolithidae (p. 181)

Bearing silicious skeleton. Family 5 Silicoflagellidae (p. 181)

Family 1 **Chromulinidae** Engler

Minute forms, naked or with sculptured shell; with a single flagellum; often with rhizopodia; a few colonial; free-swimming or attached.

Genus **Chromulina** Cienkowski. Oval; round in cross-section; amoeboid; 1–2 chromatophores; palmella stage often large; in fresh water. Numerous species. The presence of a large number of these organisms gives a golden-brown color to the surface of the water.

C. pascheri Hofeneder (Fig. 85, *a, b*). 15–20 μ in diameter.

Genus **Chrysapsis** Pascher. Solitary; plastic or rigid; chromatophore diffused or branching; with stigma; amoeboid movement; holophytic, holozoic; fresh water.

C. sagene P. (Fig. 85, *c*). Anterior region actively plastic; stigma small; 8–14 μ long; flagellum about 30 μ long.

Genus **Chrysococcus** Klebs. Shell spheroidal or ovoidal, smooth or sculptured and often brown-colored; through an opening a flagellum protrudes; 1–2 chromatophores; one of the daughter individuals formed by binary fission leaves the parent shell and forms a new one; fresh water.

C. ornatus Pascher (Fig. 85, *d*). 14–16 μ by 7–10 μ .

Genus **Mallomonas** Perty (*Pseudomallomonas* Chodat). Body elongated; with silicious scales and often spines; 2 chromatophores, rod-shaped; fresh water. Numerous species.

M. litomosa Stokes (Fig. 85, *e*). Scales very delicate, needle-like projections at both ends; flagellum as long as body; 24–32 μ by 8 μ .

Genus **Pyramidochrysis** Pascher. Body form constant; pyriform with 3 longitudinal ridges; flagellate end drawn out; a single chromatophore; 2 contractile vacuoles; fresh water.

P. modesta P. (Fig. 85, *f*). 11–13 μ long.

Genus **Sphaleromantis** Pascher. Triangular or heart-shaped; highly flattened; slightly plastic; 2 chromatophores; 2 contractile vacuoles; stigma large; long flagellum; fresh water.

S. ochracea P. (Fig. 85, *g*). 6–13 μ long.

Genus **Kephyrion** Pascher. With oval or fusiform lorica; body fills posterior half of lorica; one chromatophore; a single short flagellum; small; fresh water.

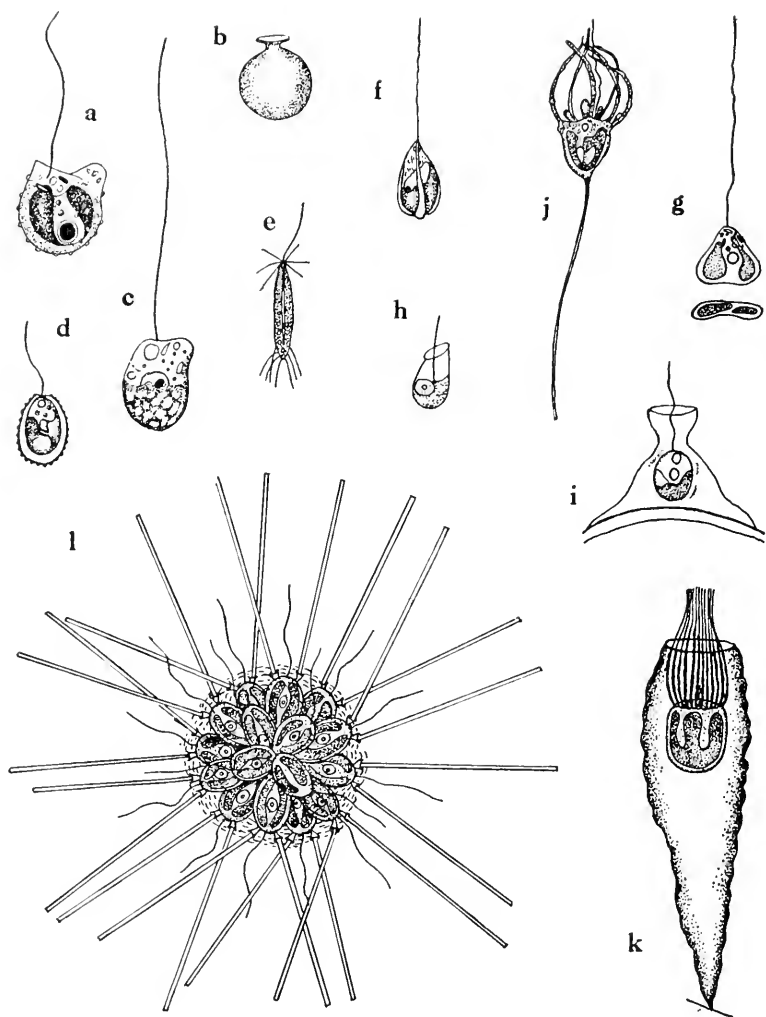


FIG. 85. a, b, *Chromulina pascheri*, $\times 670$ (Hofeneder); c, *Chrysapsis sagene*, $\times 1000$ (Pascher); d, *Chrysococcus ornatus*, $\times 600$ (Pascher); e, *Mallomonas litomosa*, $\times 400$ (Stokes); f, *Pyramidochrysis modesta*, $\times 670$ (Pascher); g, *Sphaleromantis ochracea*, $\times 600$ (Pascher); h, *Kephyrion ovum*, $\times 1600$ (Pascher); i, *Chrysopyxis cyathus*, $\times 600$ (Pascher); j, *Cyrtophora pedicellata*, $\times 400$ (Pascher); k, *Palatinella cyrtophora*, $\times 400$ (Lauterborn); l, *Chrysosphaerella longispina*, $\times 600$ (Lauterborn).

K. ovum P. (Fig. 85, *h*). Lorica up to 7μ by 4μ .

Genus **Chrysopyxis** Stein. With lorica of various forms, more or less flattened; 1–2 chromatophores; a flagellum; attached to algae in fresh water.

C. cyathus Pascher (Fig. 85, *i*). One chromatophore; flagellum twice body length; lorica $20\text{--}25\mu$ by $12\text{--}15\mu$.

Genus **Cyrtophora** Pascher. Body inverted pyramid with 6–8 tentacles and a single flagellum; with a contractile stalk; a single chromatophore; a contractile vacuole; fresh water.

C. pedicellata P. (Fig. 85, *j*). Body $18\text{--}22\mu$ long; tentacles $40\text{--}60\mu$ long; stalk $50\text{--}80\mu$ long.

Genus **Palatinella** Lauterborn. Lorica tubular; body heart-shaped; anterior border with 16–20 tentacles; a single flagellum; a chromatophore; several contractile vacuoles; fresh water.

P. cyrtophora L. (Fig. 85, *k*). Lorica $80\text{--}150\mu$ long; body $20\text{--}25\mu$ by $18\text{--}25\mu$; tentacles 50μ long.

Genus **Chrysosphaerella** Lauterborn. In spherical colony, individual cell, oval or pyriform, with 2 chromatophores; imbedded in gelatinous mass; fresh water.

C. longispina L. (Fig. 85, *l*). Individuals up to 15μ by 9μ ; colony up to 250μ in diameter; in standing water rich in vegetation.

Family 2 Syncryptidae Poche

Solitary or colonial chrysomonads with 2 equal flagella; with or without pellicle (when present, often sculptured); some possess stalk.

Genus **Syncrypta** Ehrenberg. Spherical colonies; individuals with 2 lateral chromatophores, embedded in a gelatinous mass; 2 contractile vacuoles; without stigma; cysts unknown; fresh water.

S. volvox E. (Fig. 86, *a*). $8\text{--}14\mu$ by $7\text{--}12\mu$; colony $20\text{--}70\mu$ in diameter; in standing water.

Genus **Synura** Ehrenberg. Spherical or ellipsoidal colony composed of 2–50 ovoid individuals arranged radially; body usually covered by short bristles; 2 chromatophores lateral; no stigma; asexual reproduction of individuals is by longitudinal division; that of colony by bipartition; cysts spherical; fresh water.

S. uvella E. (Fig. 86, *b*). Cells oval; bristles conspicuous; $20\text{--}40\mu$ by $8\text{--}17\mu$; colony $100\text{--}400\mu$ in diameter; if present in large numbers, the organism is said to be responsible for an odor of the water resembling that of ripe cucumber (Moore).

S. adamsi Smith (Fig. 86, c). Spherical colony with individuals radiating; individuals long spindle, $42\text{--}47\mu$ by $6.5\text{--}7\mu$; 2 flagella up to 17μ long; in fresh water pond.

Genus **Hymenomonas** Stein. Solitary; ellipsoid to cylindrical; membrane brownish, often sculptured; 2 chromatophores; without stigma; a contractile vacuole anterior; fresh water.

H. roseola S. (Fig. 86, d). $17\text{--}50\mu$ by $10\text{--}20\mu$.

Genus **Derepyxis** Stokes. With cellulose lorica, with or without short stalk; body ellipsoid to spherical with 1–2 chromatophores; 2 equal flagella; fresh water.

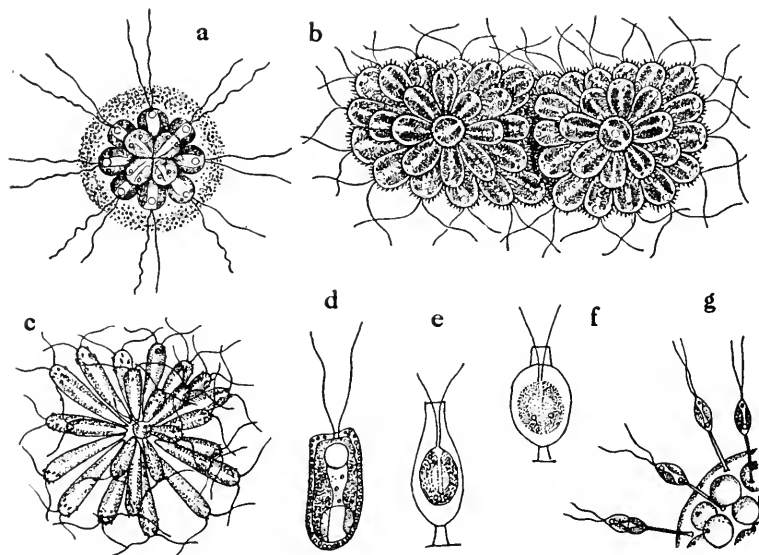


FIG. 86. a, *Synecrypta volvox*, $\times 430$ (Stein); b, *Synura uella*, $\times 500$ (Stein); c, *S. adamsi*, $\times 280$ (Smith); d, *Hymenomonas roseola*, $\times 400$ (Klebs); e, *Derepyxis amphora*, $\times 540$ (Stokes); f, *D. ollula*, $\times 600$ (Stokes); g, *Stylochrysallis parasitica*, $\times 430$ (Stein).

D. amphora S. (Fig. 86, e). Lorica $25\text{--}30\mu$ by $9\text{--}18\mu$; on algae in standing water.

D. ollula S. (Fig. 86, f). Lorica $20\text{--}25\mu$ by 15μ .

Genus **Stylochrysallis** Stein. Body fusiform; with a gelatinous stalk attached to Volvocidae; 2 equal flagella; 2 chromatophores; without stigma; fresh water.

S. parasita S. (Fig. 86, g). Body $9\text{--}11\mu$ long; stalk about 15μ long; on phytomonads.

Family 3 **Ochromonadidae** Pascher

With 2 unequal flagella; body has no pellicle and is plastic; contractile vacuoles simple; with or without delicate test; solitary or colonial; free-swimming or attached.

Genus **Ochromonas** Wyssotzki. Solitary or colonial; body surface delicate; posterior end often drawn out for attachment; 1–2 chromatophores; usually with a stigma; encystment; fresh water.

O. mutabilis Klebs (Fig. 87, *a*). Ovoid to spherical; plastic; 15–30 μ by 8–22 μ .

O. ludibunda Pascher (Fig. 87, *b*). Not plastic; 12–17 μ by 6–12 μ .

Genus **Uroglena** Ehrenberg. Spherical or ovoidal colony, composed of ovoid or ellipsoidal individuals arranged on periphery of a gelatinous mass; all individuals connected with one another by gelatinous processes running inward and meeting in a point; with a stigma and a plate-like chromatophore; asexual reproduction of individuals by longitudinal fission, that of colony by bipartition; cysts spherical with spinous projections, and a long tubular process; fresh water. One species.

U. volvox E. (Fig. 87, *c*). Cells 12–20 μ by 8–13 μ ; colony 40–400 μ in diameter; in standing water.

Genus **Uroglenopsis** Lemmermann. Similar to *Uroglena*, but individuals without inner connecting processes.

U. americana (Calkins) (Fig. 87, *d*). Each cell with one chromatophore; 5–8 μ long; flagellum up to 32 μ long; colony up to 300 μ in diameter; when present in abundance, the organism gives an offensive odor to the water (Calkins).

U. europaea Pascher. Similar to the last-named species; but chromatophores 2; cells up to 7 μ long; colony 150–300 μ in diameter.

Genus **Cyclonexis** Stokes. Wheel-like colony, composed of 10–20 wedge-shaped individuals; young colony funnel-shaped; chromatophores 2, lateral; no stigma; reproduction and encystment unknown; fresh water.

C. annularis S. (Fig. 87, *e*). Cells 11–14 μ long; colony 25–30 μ in diameter; in marshy water with sphagnum.

Genus **Dinobryon** Ehrenberg. Solitary or colonial; individuals with vase-like, hyaline, but sometimes, yellowish cellulose test, drawn out at its base; elongated and attached to the base of test

with its attenuated posterior tip; 1-2 lateral chromatophores; usually with a stigma; asexual reproduction by binary fission; one of the daughter individuals leaving test as a swarmer, to form a new one; in colonial forms daughter individuals remain attached

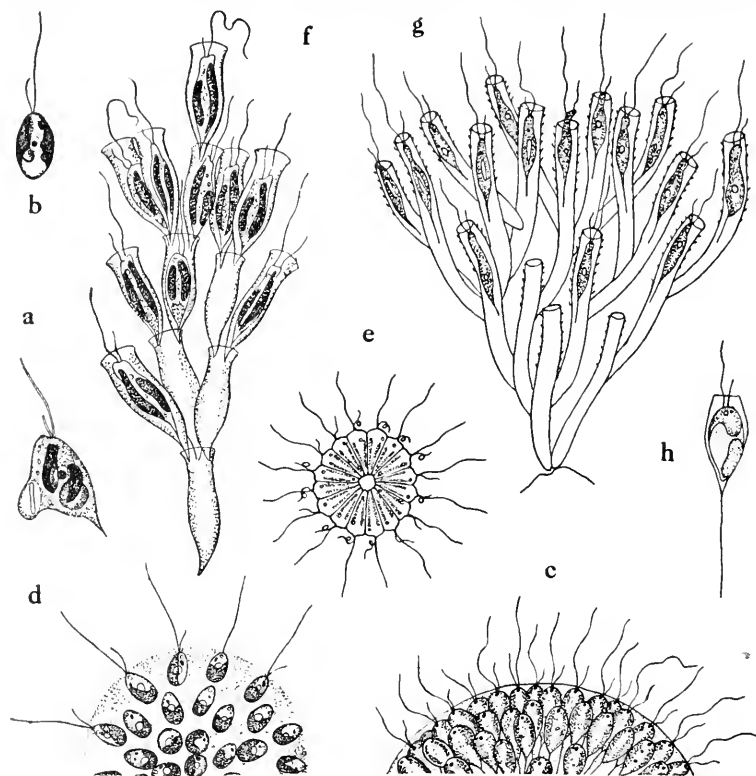


FIG. 87. a, *Ochromonas mutabilis*, $\times 670$ (Senn); b, *O. ludibunda*, $\times 540$ (Pascher); c, *Uroglena volvox*, $\times 430$ (Stein); d, *Uroglenopsis americana*, $\times 470$ (Lemmermann); e, *Cyclonexis annularis*, $\times 540$ (Stokes); f, *Dinobryon sertularia*, $\times 670$ (Scherffel); g, *Hyalobryon ramosum*, $\times 540$ (Lauterborn); h, *Stylopyxis mucicola*, $\times 470$ (Bolchonzew).

to the inner margin of aperture of parent tests and there secrete new tests; encystment common; the spherical cysts possess a short process; Ahlstrom (1937) studied variability of North American species and found the organisms occur more commonly in alkaline regions than elsewhere; fresh water. Numerous species.

D. sertularia E. (Fig. 87, f). 30–44 μ by 10–14 μ .

D. divergens Imhof. 31–53 μ long; great variation in different localities (Ahlstrom).

Genus **Hyalobryon** Lauterborn. Solitary or colonial; individual body structure similar to that of *Dinobryon*; lorica in some cases tubular, and those of young individuals are attached to the exterior of parent tests; fresh water.

H. ramosum L. (Fig. 87, g). Lorica 50–70 μ long by 5–9 μ in diameter; body up to 30 μ by 5 μ ; on vegetation in standing fresh water.

Genus **Stylopyxis** Bolochozew. Solitary; body located at bottom of a delicate stalked lorica with a wide aperture; 2 lateral chromatophores; fresh water.

S. mucicola B. (Fig. 87, h). Lorica 17–18 μ long; stalk about 33 μ long; body 9–11 μ long; fresh water.

Family 4 Cocolithidae Lohmann

The members of this family, with a few exceptions, occur in salt water only; with perforate (tremalith) or imperforate (discolith) discs, composed of calcium carbonate; 1–2 flagella; 2 yellowish chromatophores; a single nucleus; oil drops and leucosin; holophytic. Examples:

Pontosphaera haeckeli Lohmann (Fig. 88, a).

Discosphaera tubifer Murray et Blackman (Fig. 88, b).

Family 5 Silicoflagellidae Borgert

Exclusively marine planktons; with siliceous skeleton which envelops the body. Example: *Distephanus speculum* (Müller) (Fig. 88, c).

Suborder 2 Rhizochrysidina Pascher

No flagellate stage is known to occur; the organism possesses pseudopodia; highly provisional group, based wholly upon the absence of flagella; naked or with test; various forms; in some species chromatophores are entirely lacking, so that the organisms resemble some members of the Sarcodina. Several genera.

Genus **Rhizochrysis** Pascher. Body naked and amoeboid; with 1–2 chromatophores; fresh water.

R. scherffeli P. (Fig. 88, d). 10–14 μ in diameter; 1–2 chromatophores; branching rhizopods; fresh water.

Genus **Chrysidiastrum** Lauterborn. Naked; spherical; often

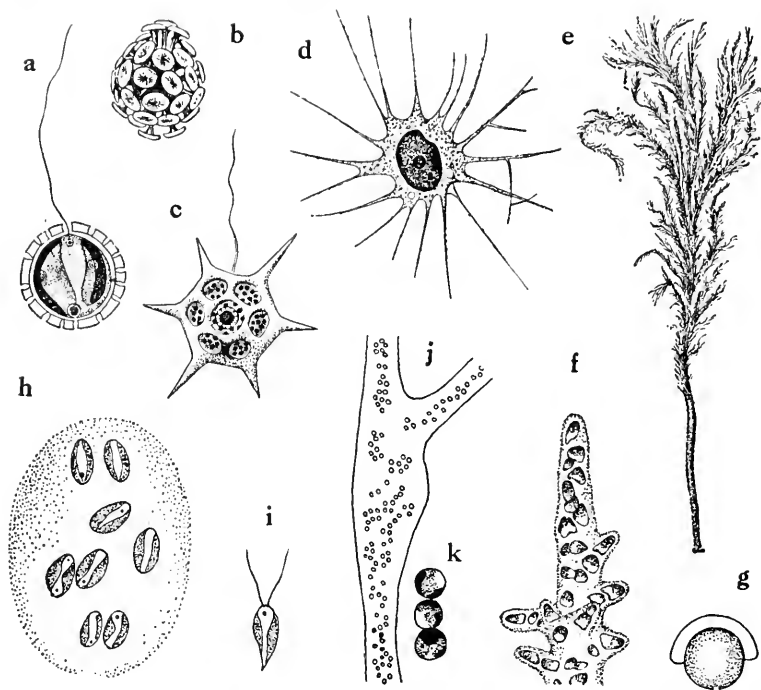


FIG. 88. a, *Pontosphaera haeckeli*, $\times 1070$ (Kühn); b, *Discosphaera tubifer*, $\times 670$ (Kühn); c, *Distephanus speculum*, $\times 530$ (Kühn); d, *Rhizochrysis scherffeli*, $\times 670$ (Doflein); e-g, *Hydrurus foetidus* (e, entire colony; f, portion; g, cyst), e (Berthold), f, $\times 330$, g, $\times 800$ (Klebs); h, i, *Chrysocapsa paludosa*, $\times 530$ (West); j, k, *Phaeosphaera gelatinosa* (j, part of a mass, $\times 70$; k, three cells, $\times 330$) (West).

several in linear association by pseudopodia; one yellow-brown chromatophore; fresh water.

C. catenatum L. Cells $12-14\mu$ in diameter.

Suborder 3 **Chrysocapsina** Pascher

Palmella stage prominent; flagellate forms transient; colonial; individuals enclosed in a gelatinous mass; 1-2 flagella, one chromatophore, and a contractile vacuole; one group of relatively minute forms and the other of large organisms.

Genus **Hydrurus** Agardh. In a large (1-30 cm. long) branching gelatinous cylindrical mass; cells yellowish brown; spherical to ellipsoidal; with a chromatophore; individuals arranged loosely

in gelatinous matrix; apical growth resembles much higher algae; multiplication of individuals results in formation of pyramidal forms with a flagellum, a chromatophore, and a leucosin mass; cyst may show a wing-like rim; cold freshwater streams.

H. foetidus Kirschner (Figs. 31, *d-f*; 88, *e-g*). Olive-green, feathery tufts, 1–30 cm. long, develops an offensive odor; sticky to touch; occasionally encrusted with calcium carbonate; in running fresh water.

Genus **Chrysocapsa** Pascher. In a spherical to ellipsoidal gelatinous mass; cells spherical to ellipsoid; 1–2 chromatophores; with or without stigma; freshwater.

C. paludosa P. (Fig. 88, *h, i*). Spherical or ellipsoidal with cells distributed without order; with a stigma; 2 chromatophores; swarmer pyriform with 2 flagella; cells 11μ long; colony up to 100μ in diameter.

Genus **Phaeosphaera** West et West. In a simple or branching cylindrical gelatinous mass; cells spherical with a single chromatophore; fresh water.

P. gelatinosa W. et W. (Fig. 88, *j, k*). Cells $14-17.5\mu$ in diameter.

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CHAPTER 8

Order 2 **Cryptomonadina** Stein

THE cryptomonads differ from the chrysomonads in having a constant body form. Pseudopodia are very rarely formed, as the body is covered by a pellicle. The majority show dorso-ventral differentiation, with an oblique longitudinal furrow. 1-2 unequal flagella arise from the furrow or from the cytopharynx. In case 2 flagella are present, both may be directed anteriorly or one posteriorly. These organisms are free-swimming or creeping.

1-2 chromatophores are usually present. They are discoid or band-form. The color of chromatophores vary from common brown, red, olive-green up to blue-green. The nature of the pigment is not well understood, but it is said to be similar to that which is found in the Dinoflagellata (Pascher). One or more spherical pyrenoids which are enclosed within a starch envelope appear to occur outside the chromatophores. Nutrition is mostly holophytic; a few saprozoic or holozoic. Assimilation products are solid discoid carbohydrates which stain blue with iodine in *Cryptomonas* or which stain reddish violet by iodine as in *Cryptochrysis*; fat and starch are produced in holozoic forms which feed upon bacteria and small Protozoa. The stigma is usually associated with the insertion point of the flagella. Contractile vacuoles, one to several, are simple and are situated near the cytopharynx. A single vesicular nucleus is ordinarily located near the middle of the body.

Asexual reproduction, by longitudinal fission, takes place in either the active or the non-motile stage. Sexual reproduction is unknown. Some cryptomonads form palmella stage and others gelatinous aggregates. In the suborder Phaeocapsina, the palmella stage is permanent. Cysts are spherical, and the cyst wall is composed of cellulose. The *Cryptomonadina* occur in fresh or sea water, living also often as symbionts in marine organisms.

Flagellate forms predominant.
.....Suborder 1 *Eucryptomonadina* (p. 185)
Palmella stage permanent.Suborder 2 *Phaeocapsina* (p. 187)

Suborder 1 **Eucryptomonadina** Pascher

Truncate anteriorly; 2 anterior flagella; with an oblique furrow near anterior end..... Family 1 Cryptomonadidae
 Reniform; with 2 lateral flagella; furrow equatorial.....
 Family 2 Nephroselmidae (p. 186)

Family 1 **Cryptomonadidae** Stein

Genus **Cryptomonas** Ehrenberg. Body elliptical with a firm pellicle; anterior end truncate; dorsal side convex, ventral side slightly so or flat; nucleus posterior; longitudinal furrow; tubular cavity extending to the middle of body, through which equally long flagella arise; 2 lateral chromatophores vary in color from green to blue-green, brown or rarely red; holophytic; with small starch-like bodies which stain blue in iodine; 1-3 contractile vacuoles anterior; fresh water. Several species.

C. ovata E. (Fig. 89, a). 20-30 μ long; among vegetation.

Genus **Chilomonas** Ehrenberg. Similar to *Cryptomonas* in general body form and structure, but colorless because of the absence of chromatophores; without pyrenoid; cytopharynx deep, lower half marked by "rudimentary trichocysts"; 1-2 contractile vacuoles, anterior; nucleus in posterior half; endoplasm often filled with polygonal starch grains; fresh water.

C. paramecium E. (Fig. 89, b). Posterior end narrowed, slightly bent "dorsally"; 20-40 μ long; saprozoic; widely distributed in stagnant water and hay infusion.

C. oblonga Pascher. Oblong; posterior end broadly rounded; 20-50 μ long.

Genus **Chrysidella** Pascher. Somewhat similar to *Cryptomonas*, but much smaller; yellow chromatophores much shorter; those occurring in Foraminifera or Radiolaria as symbionts are known as **Zooxanthellae**. Several species.

C. schaudinni (Winter) (Fig. 89, c, d). Body less than 10 μ long; in the foraminiferan *Peneroplis pertusus*.

Genus **Cyathomonas** Fromentel. Body small, somewhat oval; without chromatophores; much flattened; anterior end obliquely truncate; with 2 equal or subequal anterior flagella; colorless; nucleus central; anabolic products, stained red or reddish violet by iodine; contractile vacuole usually anterior; a row of refractile granules, protrichocysts (p. 65), close and parallel to anterior margin of body; asexual reproduction by longitudinal fission; holozoic; in stagnant water and infusion. One species.

C. truncata Ehrenberg (Fig. 89, *e*). 15–30 μ long.

Genus **Cryptochrysis** Pascher. Furrow indistinctly granulated; 2 or more chromatophores brownish, olive-green, or dark green, rarely red; pyrenoid central; 2 equal flagella; some lose flagella and may assume amoeboid form; fresh water.

C. commutata P. (Fig. 89, *f*). Bean-shaped; 2 chromatophores; 19 μ by 10 μ .

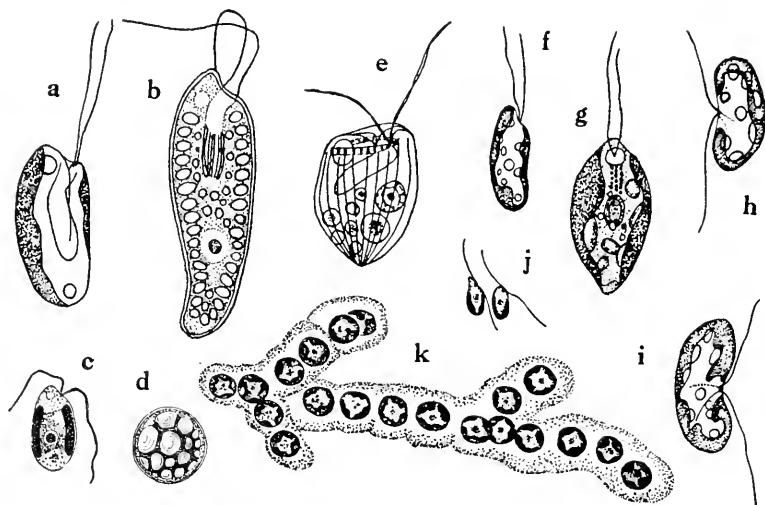


FIG. 89. a, *Cryptomonas ovata*, $\times 800$ (Pascher); b, *Chilomonas paramecium*, $\times 1330$ (Bütschli); c, d, *Chrysidella schaudinni*, $\times 1330$ (Winter); e, *Cyathomonas truncata*, $\times 670$ (Uehla); f, *Cryptochrysis commutata*, $\times 670$ (Pascher); g, *Rhodomonas lens*, $\times 1330$ (Ruttner); h, *Nephroselmis olvacea*, $\times 670$ (Pascher); i, *Protochrysis phacophycearum*, $\times 800$ (Pascher); j, k, *Phaeothamnion confervicolum*, $\times 600$ (Kühn).

Genus **Rhodomonas** Karsten. Furrow granulated; chromatophore one, red (upon degeneration the coloring matter becomes dissolved in water); pyrenoid central; fresh water.

R. lens Pascher et Ruttner (Fig. 89, *g*). Spindle-form; about 16 μ long; in fresh water.

Family 2 Nephroselmidae Pascher

Body reniform; with lateral equatorial furrow; 2 flagella arising from furrow, one directed anteriorly and the other posteriorly.

Genus **Nephroselmis** Stein. Reniform; flattened; furrow and cytopharynx distinct; no stigma; 1–2 chromatophores, discoid,

brownish green; nucleus dorsal; a central pyrenoid; 2 contractile vacuoles; with reddish globules; fresh water.

N. olvacea S. (Fig. 89, *h*). 20–25 μ by 15 μ .

Genus **Protochrysis** Pascher. Reniform; not flattened; with a distinct furrow, but without cytopharynx; a stigma at base of flagella; 1–2 chromatophores, brownish yellow; pyrenoid central; 2 contractile vacuoles; fission seems to take place during the resting stage; fresh water.

P. phaeophycearum P. (Fig. 89, *i*). 15–17 μ by 7–9 μ .

Suborder 2 **Phaeocapsina** Pascher

Palmella stage predominant; perhaps border-line forms between brown algae and cryptomonads. Example: *Phaeothamnion confervicolum* Lagerheim (Fig. 89, *j*, *k*) which is less than 10 μ long.

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CHAPTER 9

Order 3 **Phytomonadina** Blochmann

THE phytomonads are small, more or less rounded, green flagellates with a close resemblance to the algae. They show a definite body form, and most of them possess a cellulose membrane, which is thick in some and thin in others. There is a definite opening in the membrane at the anterior end, through which 1-2 (or seldom 4 or more) flagella protrude. The majority possess numerous grass-green chromatophores, each of which contains one or more pyrenoids. The method of nutrition is mostly holophytic or mixotrophic; some colorless forms are, however, saprozoic. The metabolic products are usually starch and oils. Some phytomonads are stained red, owing to the presence of haematochrome. The contractile vacuoles may be located in the anterior part or scattered throughout the body. The nucleus is ordinarily centrally located, and its division seems to be mitotic, chromosomes having been definitely noted in several species.

Asexual reproduction is by longitudinal fission, and the daughter individuals remain within the parent membrane for some time. Sexual reproduction seems to occur widely. Colony formation also occurs, especially in the family Volvocidae. Encystment and formation of the palmella stage are common among many forms. The phytomonads have a much wider distribution in fresh than in salt water.

Solitary

- Membrane a single piece; rarely indistinct
 - 2 flagella. Family 1 Chlamydomonadidae
 - 3 flagella. Family 2 Trichlorididae (p. 193)
 - 4 flagella. Family 3 Carteriidae (p. 194)
 - 5 flagella. Family 4 Chlorasteridae (p. 196)
 - 6 or more flagella. Family 5 Polyblepharididae (p. 196)
- Membrane bivalve. Family 6 Phacotidae (p. 196)
- Colonial, of 4 or more individuals; 2 (1 or 4) flagella.
..... Family 7 Volvocidae (p. 197)

Family 1 **Chlamydomonadidae** Bütschli

Solitary; spheroid, oval, or ellipsoid; with a cellulose membrane; 2 flagella; chromatophores, stigma, and pyrenoids usually present.

Genus **Chlamydomonas** Ehrenberg. Spherical, ovoid or elongated; sometimes flattened; 2 flagella; membrane often thickened at anterior end; a large chromatophore, containing one or more pyrenoids; stigma; a single nucleus; 2 contractile vacuoles anterior; asexual reproduction and palmella formation known; sexual reproduction isogamy or anisogamy; fresh water. Numerous species.

C. monadina Stein (Fig. 90, *a-c*). 15–30 μ long; fresh water; Landacre noted that the organisms obstructed the sand filters used in connection with a septic tank, together with the diatom *Navicula*.

C. angulosa Dill. About 20 μ by 12–15 μ ; fresh water.

C. epiphytica Smith (Fig. 90, *d*). 8–9 μ by 7–8 μ ; in freshwater lakes.

C. globosa Snow (Fig. 90, *e*). Spheroid or ellipsoid; 5–7 μ in diameter; in freshwater lakes.

C. gracilis Snow (Fig. 90, *f*). 10–13 μ by 5–7 μ ; fresh water.

Genus **Haematococcus** Agardh (*Sphaerella* Sommerfeldt). Spheroidal or ovoid with a gelatinous envelope; chromatophores peripheral and reticulate, with 2–8 scattered pyrenoids; several contractile vacuoles; haematochrome frequently abundant in both motile and encysted stages; asexual reproduction in motile form; sexual reproduction isogamy; fresh water.

H. pluvialis (Flotow) (Figs. 38; 90, *g*). Oval or ellipsoid; with numerous radial cytoplasmic processes; chromatophores thick-walled; body up to 60 μ by 50 μ ; stigma about 13 μ long; fresh water; according to Reichenow (1909), the haematochrome disappears under experimental condition if the culture medium is rich in nitrogen and phosphorus.

Genus **Sphaerellopsis** Korschikoff (*Chlamydococcus* Stein). With gelatinous envelope which is usually ellipsoid with rounded ends; body elongate fusiform or pyriform, no protoplasmic processes to envelope; 2 equally long flagella; chromatophore large; a pyrenoid; with or without stigma; nucleus in anterior half; 2 contractile vacuoles; fresh water.

S. fluviatilis (Stein) (Fig. 90, *h*). 14–30 μ by 10–20 μ ; fresh water.

Genus **Brachiomonas** Bohlin. Lobate; with horn-like processes, all directed posteriorly; contractile vacuoles; ill-defined chromatophore; pyrenoids; with or without stigma; sexual and asexual reproduction; fresh, brackish or salt water.

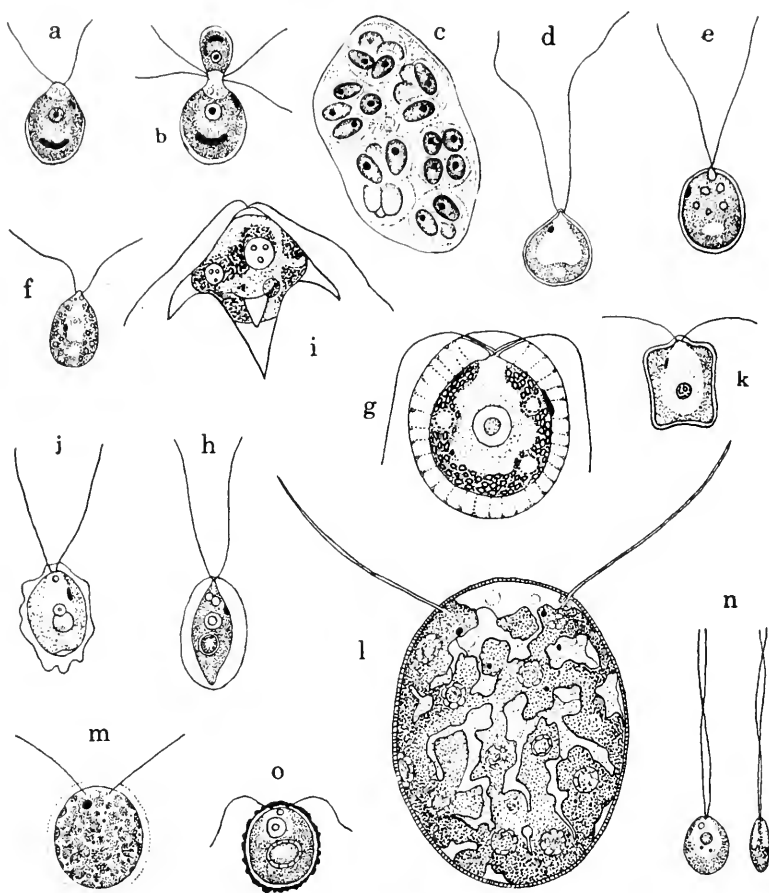


FIG. 90. a-c, *Chlamydomonas monadina*, $\times 470$ (Gorosehankin); d, *C. epiphytica*, $\times 1030$ (Smith); e, *C. globosa*, $\times 2000$ (Snow); f, *C. gracilis*, $\times 770$ (Snow); g, *Haematococcus pluvialis*, $\times 500$ (Reichenow); h, *Sphaerellopsis fluvialis*, $\times 490$ (Korschikoff); i, *Brachimonas vestiana*, $\times 960$ (West); j, *Lobomonas rostrata*, $\times 1335$ (Hazen); k, *Diplostauron pentagonium*, $\times 1110$ (Hazen); l, *Gigantochloris permaxima*, $\times 370$ (Pascher); m, *Glocomonas ovalis*, $\times 330$ (Pascher); n, *Scourfieldia complanata*, $\times 1540$ (West); o, *Thorakomonas sabulosa*, $\times 670$ (Korschikoff).

B. vestiana Pascher (Fig. 90, i). $15-24\mu$ by $13-23\mu$; brackish water.

Genus **Lobomonas** Dangeard. Ovoid or irregularly angular;

chromatophore cup-shaped; pyrenoid; stigma; a contractile vacuole; fresh water.

L. rostrata Hazen (Fig. 90, *j*). 5–12 μ by 4–8 μ .

Genus **Diplostauron** Korschikoff. Rectangular with raised corners; 2 equally long flagella; chromatophore; one pyrenoid; stigma; 2 contractile vacuoles anterior; fresh water.

D. pentagonium (Hazen) (Fig. 90, *k*). 10–13 μ by 9–10 μ .

Genus **Gigantochloris** Pascher. Unusually large form, equalling in size a colony of *Eudorina*; flattened; oval in front view; elongate ellipsoid in profile; membrane radially striated; 2 flagella widely apart, less than body length; chromatophore in network; numerous pyrenoids; often without stigma; in woodland pools.

G. permaxima P. (Fig. 90, *l*). 70–150 μ by 40–80 μ by 25–50 μ .

Genus **Gloeomonas** Klebs. Broadly ovoid, nearly subspherical; with a delicate membrane and a thin gelatinous envelope; 2 flagella widely apart; chromatophores numerous, circular or oval discs; pyrenoid (?); stigma; 2 contractile vacuoles, anterior; fresh water.

G. ovalis K. (Fig. 90, *m*). 38–42 μ by 23–33 μ ; gelatinous envelope over 2 μ thick.

Genus **Scourfieldia** West. Whole body flattened; ovoid in front view; membrane delicate; 2 flagella 2–5 times body length; a chromatophore; without pyrenoid or stigma; contractile vacuole anterior; nucleus central; fresh water.

S. complanata W. (Fig. 90, *n*). 5.2–5.7 μ by 4.4–4.6 μ ; fresh water.

Genus **Thorakomonas** Korschikoff. Flattened; somewhat irregularly shaped or ellipsoid in front view; membrane thick, encrusted with iron-bearing material, deep brown to black in color; protoplasmic body similar to that of *Chlamydomonas*; a chromatophore with a pyrenoid; 2 contractile vacuoles; standing fresh water.

T. sabulosa K. (Fig. 90, *o*). Up to 16 μ by 14 μ .

Genus **Coccomonas** Stein. Shell smooth; globular; body not filling intracapsular space; stigma; contractile vacuole; asexual reproduction into 4 individuals; fresh water.

C. orbicularis S. (Fig. 91, *a*). 18–25 μ in diameter; fresh water.

Genus **Chlorogonium** Ehrenberg. Fusiform; membrane thin and adheres closely to protoplasmic body; plate-like chromatophores usually present, sometimes ill-contoured; one or more

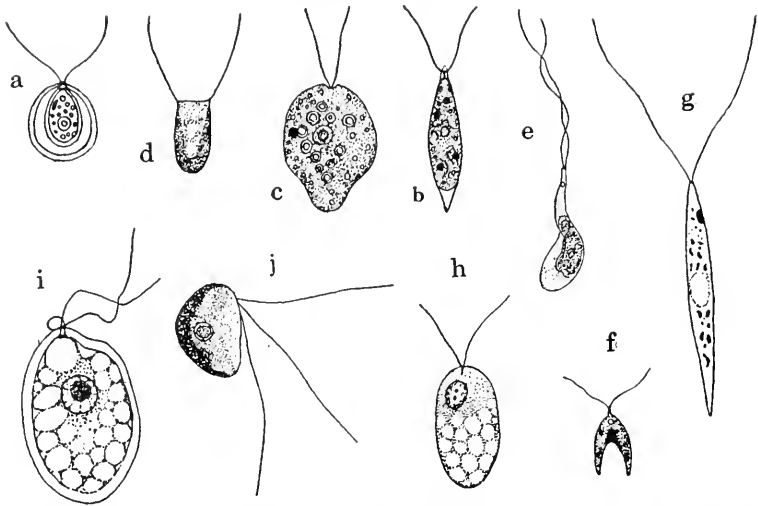


FIG. 91. a, *Coccomonas orbicularis*, $\times 500$ (Stein); b, *Chlorogonium euchlorum*, $\times 430$ (Jacobsen); c, *Phyllomonas phacoides*, $\times 200$ (Korschikoff); d, *Sphaenochloris printzi*, $\times 600$ (Printz); e, *Korschikoffia guttula*, $\times 1670$ (Pascher); f, *Furcilla lobosa*, $\times 670$ (Stokes); g, *Hyalogonium klebsi*, $\times 470$ (Klebs); h, *Polytoma urcella*, $\times 670$ (Dangeard); i, *Parapolytoma satura*, $\times 1600$ (Jameson); j, *Trichloris paradoxa*, $\times 990$ (Pascher).

pyrenoids; numerous scattered contractile vacuoles; usually a stigma; a central nucleus; asexual reproduction by 2 successive transverse fissions during motile phase; isogamy reported; fresh water.

C. euchlorum E. (Fig. 91, b). $25-70\mu$ by $4-15\mu$; in stagnant water.

Genus **Phyllomonas** Korschikoff. Extremely flattened; membrane delicate; 2 flagella; chromatophore often faded or indistinct; numerous pyrenoids; with or without stigma; many contractile vacuoles; fresh water.

P. phacoides K. (Fig. 91, c). Leaf-like; rotation movement; up to 100μ long; in standing fresh water.

Genus **Sphaenochloris** Pascher. Body truncate or concave at flagellate end in front view; sharply pointed in profile; 2 flagella widely apart; chromatophore large; pyrenoid; stigma; contractile vacuole anterior; fresh water.

S. printzi P. (Fig. 91, d). Up to 18μ by 9μ .

Genus **Korschikoffia** Pascher. Elongate pyriform with an undulating outline; anterior end narrow, posterior end more bluntly rounded; plastic; chromatophores in posterior half; stigma absent; contractile vacuole anterior; 2 equally long flagella; nucleus nearly central; salt water.

K. guttula P. (Fig. 91, *e*). 6–10 μ by 5 μ ; brackish water.

Genus **Furcilla** Stokes. U-shape, with 2 posterior processes; in side view somewhat flattened; anterior end with a papilla; 2 flagella equally long; 1–2 contractile vacuoles anterior; oil droplets; fresh water.

F. lobosa S. (Fig. 91, *f*). 11–14 μ long; fresh water.

Genus **Hyalogonium** Pascher. Elongate spindle-form; anterior end bluntly rounded; posterior end more pointed; 2 flagella; protoplasm colorless; with starch granules; a stigma; asexual reproduction results in up to 8 daughter cells; fresh water.

H. klebsi P. (Fig. 91, *g*). 30–80 μ by up to 10 μ ; stagnant water.

Genus **Polytoma** Ehrenberg (*Chlamydolepharis* Francé; *Tussetia* Pascher). Ovoid; no chromatophores; membrane yellowish to brown; pyrenoid unobserved; 2 contractile vacuoles; 2 flagella about body length; stigma if present, red or pale-colored; many starch bodies and oil droplets in posterior half of body; asexual reproduction in motile stage; isogamy; saprozoic; in stagnant fresh water.

P. uvella E. (Figs. 8, *e*; 91, *h*). Oval to pyriform; stigma may be absent; 15–30 μ by 9–20 μ .

Genus **Parapolytoma** Jameson. Anterior margin obliquely truncate, resembling a cryptomonad, but without chromatophores; without stigma and starch; division into 4 individuals within envelope; fresh water.

P. satura J. (Fig. 91, *i*). About 15 μ by 10 μ ; fresh water.

Family 2 Trichlorididae

With three flagella.

Genus **Trichloris** Scherffel et Pascher. Bean-shape; flagellate side flattened or concave; opposite side convex; chromatophore large, covering convex side; 2 pyrenoids surrounded by starch granules; a stigma near posterior end of chromatophore; nucleus central; numerous contractile vacuoles scattered; 3 flagella near anterior end.

T. paradoxa S. et P. (Fig. 91, *j*). 12–15 μ broad by 10–12 μ high; flagella up to 30 μ long.

Family 3 **Carteriidae**

With four flagella arising from anterior pole.

Genus **Carteria** Diesing (*Corbierca*, *Pithiscus*, Dangeard; *Tetramastix* Korschikoff). Ovoid, chromatophore cup-shaped; pyrenoid; stigma; 2 contractile vacuoles; fresh water. Numerous species.

C. cordiformis (Carter) (Fig. 92, *a*). Heart-shaped in front view; ovoid in profile; chromatophore large; $18\text{--}23\mu$ by $16\text{--}20\mu$.

C. ellipsoidal Bold. Ellipsoid; chromatophore; a small stigma; division into 2, 4, or 8 individuals in encysted stage; $6\text{--}24\mu$ long; fresh water, Maryland (Bold, 1938).

Genus **Pyramimonas** Schmarda (*Pyramidomonas* Stein). Small pyramidal or heart-shaped body; with bluntly drawn-out posterior end; usually 4 ridges in anterior region; 4 flagella; green chromatophores cup-shaped; with or without stigma; with a large pyrenoid in the posterior part; contractile vacuoles in the anterior portion; fresh water. Several species.

P. tetrahynchus S. (Fig. 92, *b*). $20\text{--}28\mu$ by $12\text{--}18\mu$; fresh water; Wisconsin (Smith, 1933).

P. montana Geitler. Bluntly conical; anterior end 4-lobed or truncate; posterior end narrowly rounded; plastic; pyriform nucleus anterior, closely associated with 4 flagella; stigma; 2 contractile vacuoles anterior; chromatophore cup-shaped, granular, with scattered starch grains and oil droplets; a pyrenoid with a ring of small starch grains; $17\text{--}22.5\mu$ long (Geitler); $12\text{--}20\mu$ by $8\text{--}16\mu$ (Bold), flagella about body length; fresh water, Maryland (Bold, 1938).

Genus **Polytomella** Aragão. Ellipsoid, or oval, with a small papilla at anterior end, where 4 equally long flagella arise; with stigma; starch; fresh water.

P. agilis A. (Fig. 92, *c*, *d*). Numerous starch grains; $8\text{--}18\mu$ by $5\text{--}9\mu$; flagella $12\text{--}17\mu$ long; fresh water; hay infusion.

Genus **Medusochloris** Pascher. Hollowed hemisphere with 4 processes, each bearing a flagellum at its lower edge; a lobed plate-shaped chromatophore; without pyrenoid below convex surface. One species.

M. phiale P. In salt water pools with decaying algae in the Baltic.

Genus **Spirogonium** Pascher. Body spindle-form; membrane delicate; flagella a little longer than body; chromatophore con-

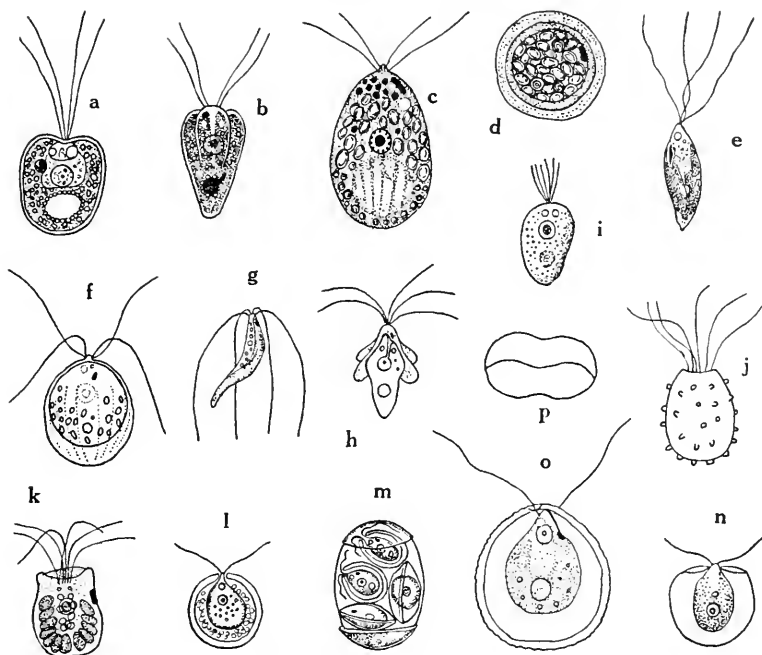


FIG. 92. a, *Carteria cordiformis*, $\times 600$ (Dill); b, *Pyramimonas tetra-rhynchus*, $\times 400$ (Dill); c, d, *Polytomella agilis*, $\times 1000$ (Doflein); e, *Spirogonium chloronioides*, $\times 670$ (Pascher); f, *Tetrablepharis multifilis*, $\times 670$ (Pascher); g, *Spermatozopsis exultans*, $\times 1630$ (Pascher); h, *Chloraster gyrans*, $\times 670$ (Stein); i, *Polyblepharides singularis*, $\times 870$ (Dangeard); j, k, *Pocillomonas flos aquae*, $\times 920$ (Stein-ecke); l, m, *Phaeotus lenticularis*, $\times 430$ (Stein); n, *Pteromonas angulosa*, $\times 670$ (West); o, p, *Dysmorphocoeus variabilis*, $\times 1000$ (Bold).

spicuous; a pyrenoid; stigma anterior; 2 contractile vacuoles; fresh water. One species.

S. chloronioides (P.) (Fig. 92, e). Body up to 25μ by 15μ .

Genus **Tetrablepharis** Senn. Ellipsoid to ovoid; pyrenoid present; other characters are those of *Polytoma*; fresh water.

T. multifilis (Klebs) (Fig. 92, f). $12-20\mu$ by $8-15\mu$; stagnant water.

Genus **Spermatozopsis** Korschikoff. Sickie-form; bent easily, occasionally plastic; chromatophore mostly on convex side; a distinct stigma at more rounded anterior end; flagella equally long; 2 contractile vacuoles anterior; fresh water infusion.

S. exultans K. (Fig. 92, g). $7-9\mu$ long; also biflagellate; in fresh water with algae, leaves, etc.

Family 4 **Chlorasteridae**

With 5 flagella arising from anterior pole.

Genus **Chloraster** Ehrenberg. Similar to *Pyramimonas*, but anterior half with a conical envelope drawn out at four corners; with 5 flagella; fresh or salt water.

C. gyraus E. (Fig. 92, *h*). Up to 18μ long; standing water; also reported from salt water.

Family 5 **Polyblepharididae** Dangeard

With 6 or more flagella arising from anterior end.

Genus **Polyblepharides** Dangeard. Ellipsoid or ovoid; flagella 6–8, shorter than body length; chromatophore; a pyrenoid; a central nucleus; 2 contractile vacuoles anterior; cysts; a questionable genus; fresh water.

P. singularis D. (Fig. 92, *i*). $10\text{--}14\mu$ by $8\text{--}9\mu$.

Genus **Pocillomonas** Steinecke. Ovoid with broadly concave anterior end; covered with gelatinous substance with numerous small projections; 6 flagella; chromatophores disc-shaped; 2 contractile vacuoles anterior; nucleus central; starch bodies; without pyrenoid.

P. flos aquae S. (Fig. 92, *j, k*). 13μ by 10μ ; fresh water pools.

Family 6 **Phacotidae** Poche

The shell typically composed of 2 valves; 2 flagella protrude from anterior end; with stigma and chromatophores; asexual reproduction within the shell; valves may become separated from each other owing to an increase in gelatinous contents.

Genus **Phacotus** Perty. Oval to circular in front view; lenticular in profile; protoplasmic body does not fill dark-colored shell completely; flagella protrude through a foramina; asexual reproduction into 2 to 8 individuals; fresh water.

P. lenticularis (Ehrenberg) (Fig. 92, *l, m*). $13\text{--}20\mu$ in diameter; in stagnant water.

Genus **Pteromonas** Seligo. Body broadly winged in plane of suture of 2 valves; protoplasmic body fills shell; chromatophore cup-shaped; one or more pyrenoids; stigma; 2 contractile vacuoles; asexual reproduction into 2–4 individuals; sexual reproduction by isogamy; zygotes usually brown; fresh water. Several species.

P. angulosa (Lemmermann) (Fig. 92, *n*). With a rounded wing

and 4 protoplasmic projections in profile; $13\text{--}17\mu$ by $9\text{--}20\mu$; fresh water.

Genus **Dysmorphococcus** Takeda. Circular in front view; anterior region narrowed; posterior end broad; shell distinctly flattened posteriorly, ornamented by numerous pores; sutural ridge without pores; 2 flagella; 2 contractile vacuoles; stigma, pyrenoid, cup-shaped chromatophore; nucleus; multiplication by binary fission; fresh water.

D. variabilis Takeda (Fig. 92, o, p). Shell $14\text{--}19\mu$ by $13\text{--}17\mu$; older shells dark brown; fresh water; Maryland (Bold, 1938).

Family 7 Volvocidae Ehrenberg

An interesting group of colonial flagellates; individual similar to Chlamydomonadidae, with 2 equally long flagella (one in Mastigophaera; 4 in Spondylomorum), green chromatophores, pyrenoids, stigma, and contractile vacuoles; body covered by a cellulose membrane and not plastic; colony or coenobium is discoid or spherical; exclusively freshwater inhabitants.

Genus **Volvox** Linnaeus. Often large spherical or subspherical colonies, consisting of a large number of cells which are differentiated into somatic and reproductive cells; somatic cells numerous, embedded in gelatinous matrix, and contains a chromatophore, one or more pyrenoids, a stigma and several contractile vacuoles; in some species protoplasmic connections occur between adjacent cells; generative cells few and large. Both mono- and bi-sexual reproduction occurs; monosexual gametes usually fewer and larger in size than bisexual ones, each producing a young colony by repeated division; bisexual reproduction anisogamy; zygotes usually brownish red in color, with smooth, undulating, or spinous envelopes; fresh water.

V. globator L. (Fig. 93, a). Ellipsoid colony, composed of 5000–20,000 cells which are $3\text{--}5\mu$ high by up to 8μ wide; monoecious; up to 800μ in diameter; in European waters.

V. perglobator Powers. Colony up to 1.5 mm. in diameter; cells resemble those of *V. globator*; in American waters.

V. aureus Ehrenberg (Figs. 71; 93, b). Dioecious; cytoplasmic threads relatively thin and long; cells pyriform, $5\text{--}9\mu$ in diameter; colony $500\text{--}800\mu$ in diameter.

V. spermatophaera Powers. Monoecious; cells number 1000–3000; without any cytoplasmic connections; colony $150\text{--}1000\mu$ in diameter.

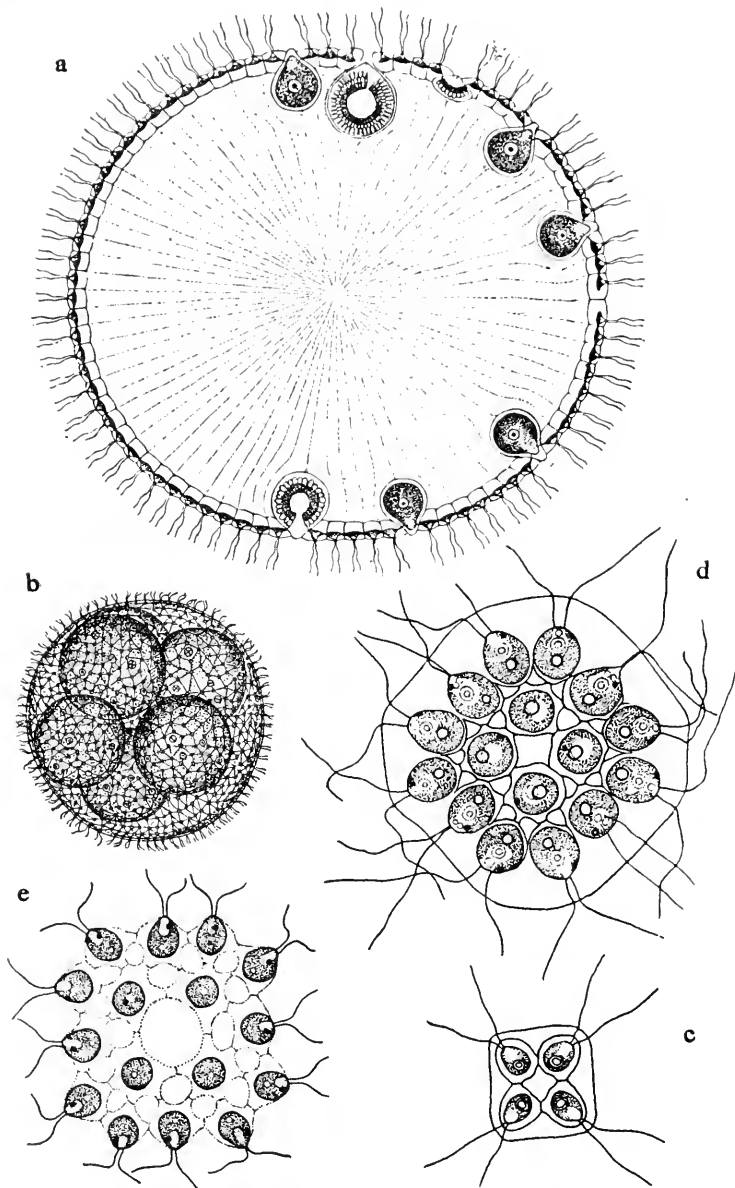


FIG. 93. a, *Volvox globator*, $\times 200$ (Janet); b, *V. aureus*, $\times 110$ (Klein); c, *Gonium sociale*, $\times 270$ (Chordat); d, *G. pectorale*, $\times 670$ (Hartmann); e, *G. formosum*, $\times 600$ (Pascher).

V. tertius Meyer. Dioecious; without cytoplasmic connections in mature state; individuals about $7-8\mu$ in diameter.

Genus **Gonium** Müller. 4 or 16 individuals arranged in one plane; cell ovoid or slightly polygonal; with 2 flagella arranged in the plane of coenobium; with or without a gelatinous envelope; protoplasmic connections among individuals occur occasionally; asexual reproduction through simultaneous divisions of component cells; sexual reproduction isogamy; zygotes reddish; fresh water.

G. sociale (Dujardin) (Fig. 93, *c*). 4 individuals form a discoid colony; cells $10-22\mu$ by $6-16\mu$ wide; in open waters of ponds and lakes.

G. pectorale M. (Fig. 93, *d*). 16 (rarely 4 or 8) individuals form a colony; 4 cells in center; 12 peripheral, closely arranged; cells $5-14\mu$ by 10μ ; colony up to 90μ in diameter; fresh water.

G. formosum Pascher (Fig. 93, *e*). 16 cells in a colony further apart; peripheral gelatinous envelope reduced; cells similar in size to those of *G. sociale* but colony somewhat larger: freshwater lakes.

Genus **Stephanoon** Schewiakoff. Spherical or ellipsoidal colony, surrounded by gelatinous envelope, and composed of 8 or 16 biflagellate cells, arranged in 2 alternating rows on equatorial plane; fresh water.

S. askenasi S. (Fig. 94, *a*). 16 individuals in ellipsoidal colony; cells 9μ in diameter; flagella up to 30μ long; colony 78μ by 60μ .

Genus **Platydorina** Kofoid. 32 cells arranged in a slightly twisted plane; flagella directed alternately to both sides; fresh water.

P. caudata K. (Fig. 94, *b*). Individual cells $10-15\mu$ long; colony up to 165μ long, 145μ wide, and 25μ thick; rivers and lakes.

Genus **Spondylomorom** Ehrenberg. 16 cells in a compact group in 4 transverse rings; each with 4 flagella; asexual reproduction by simultaneous division of component cells; fresh water. One species.

S. quaternarium E. (Fig. 94, *c*). Cells $12-26\mu$ by $8-15\mu$; colony up to 60μ long.

Genus **Chlamydobotrys** Korschikoff. Colony composed of 8 or 16 individuals; cells with 2 flagella; chromatophore; stigma; no pyrenoid; fresh water.

C. stellata K. (Fig. 94, *d*). Colony composed of 8 individuals

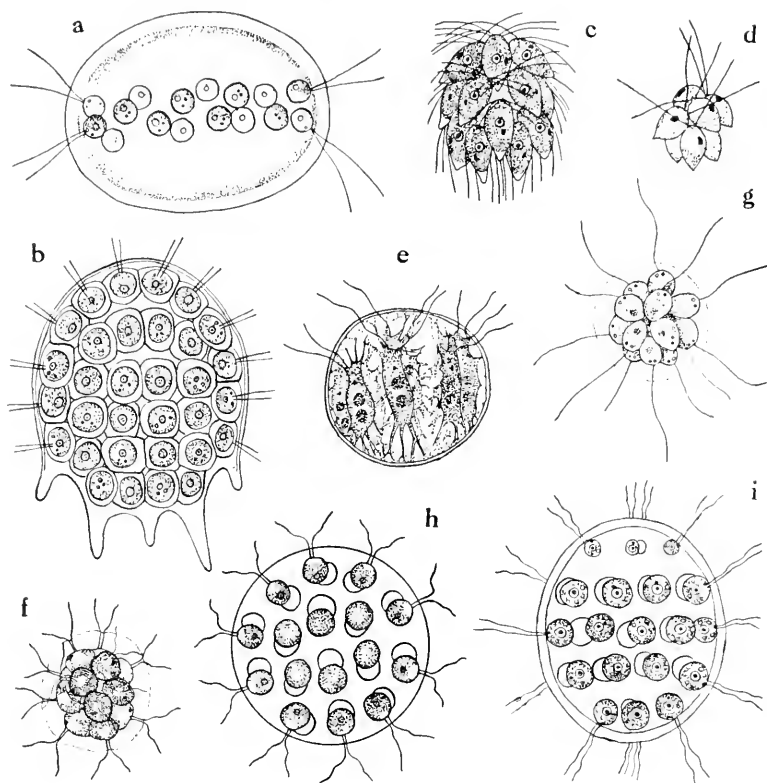


FIG. 94. a, *Stephanoon askenasi*, $\times 440$ (Schewiakoff); b, *Platydorina caudata*, $\times 280$ (Kofoid); c, *Spondylomorum quaternarium*, $\times 330$ (Stein); d, *Chlamydotrys stellata*, $\times 430$ (Korschikoff); e, *Stephanosphaera pluvialis*, $\times 250$ (Hieronymus); f, *Pandorina morum*, $\times 300$ (Smith); g, *Mastigosphaera gobii*, $\times 520$ (Schewiakoff); h, *Eudorina elegans*, $\times 310$ (Goebel); i, *Pleodorina illinoisensis*, $\times 200$ (Kofoid).

arranged in 2 rings; individuals $14\text{--}15\mu$ long; colony $30\text{--}40\mu$ in diameter; Maryland (Bold, 1933).

Genus **Stephanosphaera** Cohn. Spherical or subspherical colony, with 8 (rarely 4 or 16) cells arranged in a ring; cells pyriform, but with several processes; 2 flagella on one face; asexual reproduction and isogamy (p. 146); fresh water.

S. pluvialis C. (Figs. 70; 94, e). Cells $7\text{--}13\mu$ long; colony $30\text{--}60\mu$ in diameter.

Genus **Pandorina** Bory. Spherical or subspherical colony of usually 16 (sometimes 8 or 32) biflagellate individuals, closely packed within a gelatinous, but firm and thick matrix; individuals often angular; with stigma and chromatophores; asexual reproduction through simultaneous division of component individuals; anisogamy preceded by division of each cell into 16 to 32 gametes; zygotes colored and covered by a smooth wall; fresh water. One species.

P. morum (Müller) (Figs. 72; 94, *f*). Cells $8-17\mu$ long; colony $20-40\mu$, up to 250μ in diameter; ponds and ditches.

Genus **Mastigosphaera** Schewiakoff. Similar to *Pandorina*; but individual with a single flagellum which is 3.5 times the body length; fresh water.

M. gobii S. (Fig. 94, *g*). Individual 9μ long; colony $30-33\mu$.

Genus **Eudorina** Ehrenberg. Spherical or ellipsoidal colony of usually 32 or sometimes 16 spherical cells; asexual reproduction similar to that of *Pandorina*; isogamy with 32-64 spherical green macrogametes and numerous clustered microgametes; reddish zygote with a smooth wall; fresh water.

E. elegans E. (Figs. 73; 94, *h*). Cells $10-24\mu$ in diameter; colony $40-150\mu$ in diameter; in ponds, ditches and lakes.

Genus **Pleodorina** Shaw. Somewhat similar to *Eudorina*, being composed of 32, 64, or 128 ovoid or spherical cells of 2 types: small somatic and large generative, and are located within a gelatinous matrix; fresh water.

P. illinoisensis Kofoed (Figs. 31, *b, c*; 94, *i*). 32 cells in ellipsoid colony, 4 vegetative and 28 reproductive individuals; arranged in 5 circles, 4 in each polar circle, 8 at equator and 8 on either side of equator; 4 small vegetative cells at anterior pole; vegetative cells $10-16\mu$ in diameter; reproductive cells $19-25\mu$ in diameter; colony up to 160μ by 130μ .

P. californica S. Spherical colony with 64 or 128 cells, of which $1/2-2/3$ are reproductive cells; vegetative cells $13-15\mu$; reproductive cells up to 27μ ; colony up to 450μ , both in diameter.

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CHAPTER 10

Order 4 **Euglenoidina** Blochmann

THE body is as a rule elongated; some are plastic, others have a definite body form with a well-developed, striated or variously sculptured pellicle. At the anterior end, there is an opening through which a flagellum protrudes. In holophytic forms the to-called cytostome and cytopharynx, if present, are apparently not concerned with the food-taking, but seem to give a passage-way for the flagellum and also to excrete the waste fluid matters which become collected in one or more contractile vacuoles located around the reservoir. In holozoic forms, a well-developed cytostome and cytopharynx are present. Ordinarily there is only one flagellum, but some possess two or three. Chromatophores are present only in the majority of the Euglenidae and absent in the other two families. They are green, vary in shape, such as spheroidal, band-form, cup-form, discoidal, or fusiform, and usually possess pyrenoids. Some forms may contain haemochrome. A small but conspicuous stigma is invariably present near the anterior end of the body in chromatophore-bearing forms.

Reserve food material is the paramylon body, fat, and oil, the presence of which depends naturally on the metabolic condition of the organism. The paramylon body assumes diverse forms in different species, but is, as a rule, constant in each species, and this facilitates specific identification to a certain extent. Nutrition is holophytic in chromatophore-possessing forms, which, however, may be saprozoic, depending on the amount of light and organic substances present in the water. The holozoic forms feed upon bacteria, algae, and smaller Protozoa.

The nucleus, as a rule, is large and distinct and contains almost always a large endosome. Asexual reproduction is by longitudinal fission; sexual reproduction has been observed in a few species. Encystment is common. The majority inhabit fresh water, but some live in brackish or salt water, and a few are parasitic in animals.

With stigma.....	Family 1 Euglenidae
Without stigma	
With 1 flagellum.....	Family 2 Astasiidae (p. 209)
With 2 flagella.....	Family 3 Anisonemidae (p. 212)

Family 1 Euglenidae Stein

Body plastic ("euglenoid"), but, as a rule, more or less spindle-shaped during movement; the majority possess a single anterior flagellum (with the exception of Eutreptia and Euglenamorphs); green (sometimes red) chromatophores (except one genus) and stigma occur, though in some cases absent; metabolic products oil and paramylon; asexual reproduction by longitudinal fission in either active or resting stage; mostly freshwater inhabitants.

Genus **Euglena** Ehrenberg. Short or elongated spindle, cylindrical, or band-form; pellicle usually marked by longitudinal or spiral striae; some highly plastic with a thin pellicle; others regularly spirally twisted; stigma usually anterior; chromatophores numerous and discoid, band-form, or fusiform; pyrenoids may or may not be surrounded by starch envelope; metabolic products paramylon bodies which may be two in number; one being located on either side of nucleus, and rod-like to ovoid in shape or numerous and scattered throughout; contractile vacuoles small, near reservoir; asexual reproduction by longitudinal fission; sexual reproduction reported in *Euglena sanguinea*; common in stagnant water, especially where algae occur; when present in large numbers, the active organisms may form a green film on the surface of water and resting or encysted stages may produce conspicuous green spots on the bottom of pond or pool; in fresh water. Numerous species.

E. pisciformis Klebs (Fig. 95, *a*). 25–30 μ by 7–10 μ ; spindle-form, with bluntly pointed anterior and sharply attenuated posterior end; slightly plastic; highly active; paramylon indistinct; chromatophores lateral and discoidal; 2 pyrenoids; flagellum fairly long.

E. viridis Ehrenberg (Fig. 95, *b*). 50–60 μ by 14–18 μ ; anterior end rounded, posterior end pointed; spindle-shaped during motion, highly plastic when stationary; pellicle obliquely striated; chromatophores more or less band-form, arranged in a stellate form; nucleus posterior; nutrition holophytic, but also able to carry on saprozoic nutrition, during which period chromatophores degenerate.

E. acus E. (Figs. 24, b; 95, c). 100–200 μ long; long spindle-form; posterior end sharply pointed; flagellum short; spiral striation on pellicle very delicate; paramylon bodies rod-form; nucleus central; stigma distinct; numerous disc-like chromatophores; without pyrenoids; sluggish.

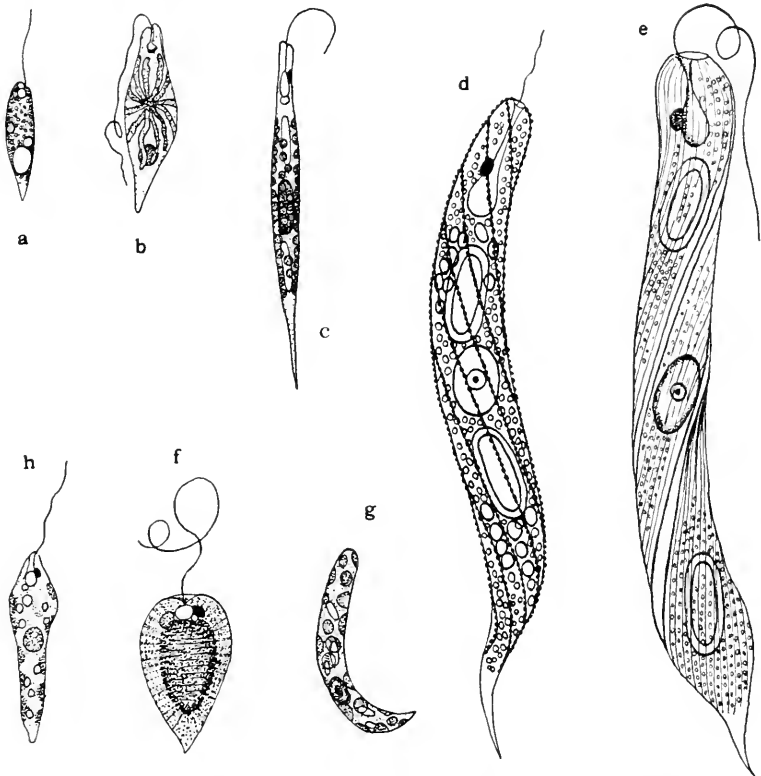


FIG. 95. a, *Euglena pisciformis*, $\times 270$ (Klebs); b, *E. viridis*, $\times 370$ (Lemmermann); c, *E. acus*, $\times 270$ (Klebs); d, *E. spirogyra*, $\times 430$ (Stein); e, *E. oxyuris*, $\times 430$ (Stein); f, *E. sanguinea*, $\times 130$ (Klebs); g, *E. deses*, $\times 230$ (Lemmermann); h, *E. gracilis*, $\times 270$ (Klebs).

E. spirogyra E. (Figs. 24, c; 95, d). 80–125 μ by 10–20 μ ; cylindrical; with spiral striae, consisting of small knobs; numerous disc-like chromatophores; without pyrenoids; 2 ovoidal paramylon bodies, one on either side of centrally located nucleus; flagellum short; stigma prominent; sluggish.

E. oxyuris Schmarda (Fig. 95, e). 375–500 μ by 30–45 μ ; almost

always spirally twisted, somewhat flattened; pellicle with spirally arranged striae; numerous chromatophores; without pyrenoids; 2 ovoid paramylon bodies conspicuously observable, one on either side of nucleus; flagellum short.

E. sanguinea E. (Figs. 37, *e-h*; 95, *f*). 55–120 μ by 28–33 μ ; with haematochrome; often found in crust on surface or half-dry bed of a pool; considered by some workers as a variety of *E. viridis*.

E. deses E. (Figs. 24, *a*; 95, *g*). 85–155 μ by 15–22 μ ; elongate, highly plastic; body striation faintly visible; stigma distinct; nucleus central, numerous chromatophores hemi-lenticular; several small rod-shaped paramylon bodies scattered; flagellum short.

E. gracilis Klebs (Figs. 37, *a-d*; 95, *h*). 37–45 μ by 6–23 μ ; cylindrical to elongated oval; highly plastic; flagellum less than body length; chromatophores numerous, discoid; nucleus central; pyrenoids.

Genus **Khawkinea** Jahn et McKibben. Similar to Genus *Euglena*, but without chromatophores and thus permanently colorless; fresh water.

K. halli J. et Mc. 40–45 μ (30–65 μ) by 12–14 μ ; fusiform; pellicle spirally striated; plastic; flagellum slightly longer than body; stigma 2–3 μ in diameter, yellow-orange to reddish-orange, composed of numerous granules; numerous (25–100) paramylon bodies elliptical or polyhedral; cysts 20–30 μ in diameter; putrid leaf infusion; saprozoic.

K. ocellata (Khawkine). Similar to above; flagellum 1.5–2 times body length; fresh water.

Genus **Phacus** Nitzsch. Highly flattened; asymmetrical; body-form constant; pellicle often with prominent longitudinal or oblique striae; a flagellum and a stigma; nucleus posterior; a short “cytopharynx”; green chromatophores rounded discoid; with or without paramylon bodies around a pyrenoid; in fresh water. Numerous species.

P. pleuronectes (Müller) (Fig. 96, *a*). 45–50 μ by 30–33 μ ; short posterior prolongation slightly curved; a prominent fold on convex side, extending to middle of body; longitudinally striated; one or more circular paramylon bodies; colorless forms sometimes appear; flagellum as long as body.

P. longicaudus (Ehrenberg) (Fig. 96, *b*). 85–115 μ by 45–70 μ ;

usually twisted with a long caudal prolongation; stigma prominent; discoidal paramylon body central; pellicle longitudinally striated.

P. pyrum (E.) (Fig. 96, c). About 40μ long; pyriform, with a straight caudal prolongation; pellicle obliquely striated.

P. triquetter (E.) (Fig. 96, d). $50\text{--}55\mu$ by $30\text{--}35\mu$; ovate; with a longitudinal ridge; posterior end acuminate; oblique striation distinct; 1–2 paramylon bodies.

P. anacoelus Stokes (Fig. 96, e). About 42μ long; oval or round; with flagellum as long as body.

P. acuminata S. (Fig. 96, f). About 25μ long; nearly circular in outline; longitudinally striated; fold long; flagellum as long as body; 2 small paramylon bodies.

Genus **Crumenula** Dujardin (*Lepocinclis* Perty). Body more or less ovo-cylindrical; rigid with spirally striated pellicle; often with a short posterior spinous projection; stigma sometimes present; numerous discoidal chromatophores marginal; paramylon bodies usually large and ring-shaped, laterally disposed; without pyrenoids; fresh water. Several species.

C. ova (Ehrenberg) (Fig. 96, g). $20\text{--}40\mu$ long; in fresh water with Euglena.

Genus **Trachelomonas** Ehrenberg. With a lorica which often possesses numerous spinous projections; sometimes yellowish to dark brown; a single flagellum protrudes from anterior aperture, the rim of which is frequently thickened to form a collar; chromatophores either 2 curved plates or numerous discs; paramylon bodies small grains; stigma and pyrenoids; multiplication by longitudinal fission; one daughter individual retains lorica and flagellum, while the other escapes through flagellar aperture, forms a new flagellum and secretes a lorica; cysts common; specific differentiation is based upon the lorica; fresh water. Numerous species.

T. hispida (Perty) (Figs. 31, a; 96, h). Lorica oval, with numerous minute spines; brownish; 8–10 chromatophores; $20\text{--}42\mu$ by $15\text{--}26\mu$; many varieties.

T. urceolata Stokes (Fig. 96, i). Lorica vasiform, smooth with a short neck; about 45μ long.

T. piscatoris (Fisher) (Fig. 96, j). Lorica cylindrical with a short neck and with numerous short, conical spines; $25\text{--}40\mu$ long; flagellum 1–2 times body length.

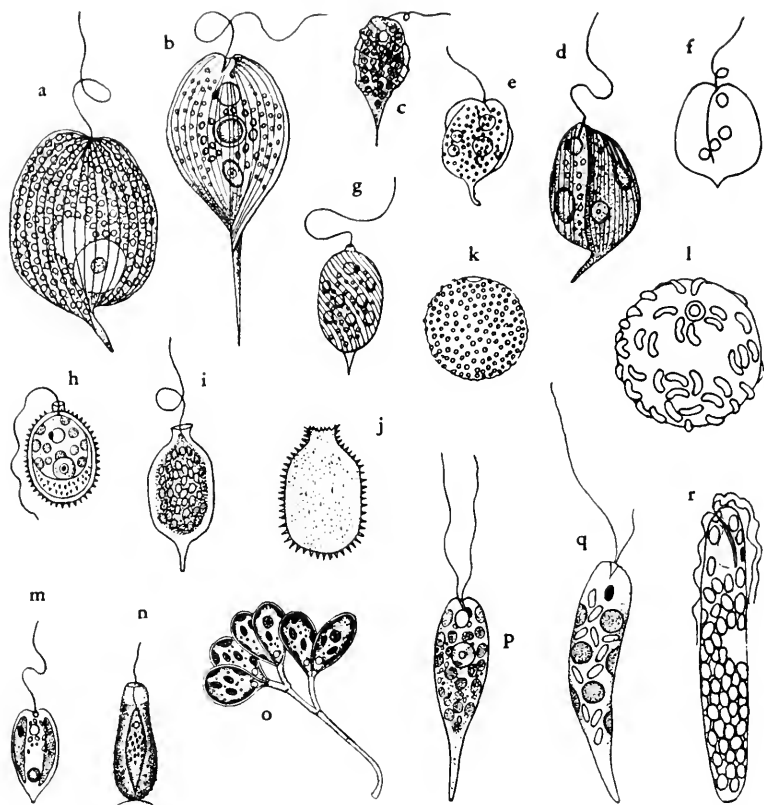


FIG. 96. a, *Phacus pleuronectes*, $\times 670$ (Lemmermann); b, *P. longicaudus*, $\times 430$ (Stein); c, *P. pyrum*, $\times 400$ (Lemmermann); d, *P. triqueter*, $\times 430$ (Stein); e, *P. anacoelus*, $\times 330$ (Stokes); f, *P. acuminata*, $\times 560$ (Stokes); g, *Crumenula ora*, $\times 430$ (Stein); h, *Trachelomonas hispida*, $\times 430$ (Stein); i, *T. urceolata*, $\times 430$ (Stokes); j, *T. piscatoris*, $\times 520$ (Fischer); k, *T. verrucosa*, $\times 550$ (Stokes); l, *T. vermiculosa*, $\times 800$ (Palmer); m, *Cryptoglena pigra*, $\times 430$ (Stein); n, *Ascoglena vaginicola*, $\times 390$ (Stein); o, *Colacium vesiculosum*, $\times 390$ (Stein); p, *Eutreptia viridis*, $\times 270$ (Klebs); q, *E. marina*, $\times 670$ (da Cunha); r, *Euglenamorpha hegneri*, $\times 730$ (Wenrich).

T. verrucosa Stokes (Fig. 96, k). Lorica spherical, with numerous knob-like attachments; no neck; $24\text{--}25\mu$ in diameter.

T. vermiculosa Palmer (Fig. 96, l). Lorica spherical; with sausage-form markings; 23μ in diameter.

Genus **Cryptoglena** Ehrenberg. Body rigid, flattened; 2 band-

form chromatophores lateral; a single flagellum; nucleus posterior; among freshwater algae. One species.

C. pigra E. (Fig. 96, *m*). Ovoid, pointed posteriorly; flagellum short; stigma prominent; $10\text{--}15\mu$ by $6\text{--}10\mu$; standing water.

Genus **Ascoglena** Stein. Encased in a flexible, colorless to brown lorica, attached with its base to foreign object; solitary, without stalk; body ovoidal, plastic; attached to test with its posterior end; a single flagellum; a stigma; numerous chromatophores discoid; with or without pyrenoids; reproduction as in *Trachelomonas* (p. 207); fresh water.

A. vaginicola S. (Fig. 96, *n*). Lorica about 43μ by 15μ .

Genus **Colacium** Ehrenberg. Stalked individuals form colony; frequently attached to animals such as copepods, rotifers, etc.; stalk mucilaginous; individual cells pyriform, ellipsoidal or cylindrical; without flagellum; a single flagellum only in free-swimming stage; discoidal chromatophores numerous; with pyrenoids; multiplication by longitudinal fission; also by swarmers, possessing a flagellum and a stigma; fresh water. Several species.

C. vesiculosum E. (Fig. 96, *o*). Colony of 2–8 cells; also solitary; $20\text{--}30\mu$ by $9\text{--}18\mu$; attached to freshwater copepods.

Genus **Eutreptia** Perty (*Eutreptiella* Cunha). With 2 flagella at anterior end; pellicle distinctly striated; plastic; spindle-shaped during movement; stigma; numerous discoid chromatophores; pyrenoids absent; paramylon bodies spherical or sub-cylindrical; multiplication as in *Euglena*; cyst with a thick stratified wall; fresh or salt water.

E. viridis P. (Fig. 96, *p*). $50\text{--}70\mu$ by $5\text{--}13\mu$; in fresh water; a variety was reported from brackish water ponds.

E. marina (da Cunha) (Fig. 96, *q*). Flagella unequal in length; longer one as long as body, shorter one $1/3$; body $40\text{--}50\mu$ by $8\text{--}10\mu$; salt water.

Genus **Euglenamorpha** Wenrich. Body form and structure similar to those of *Euglena*, but with 3 flagella; in gut of frog tadpoles. One species.

E. hegneri W. (Fig. 96, *r*). $40\text{--}50\mu$ long.

Family 2 Astasiidae Bütschli

Similar to Euglenidae in body form and general structure, but without chromatophores; body is plastic, although it assumes

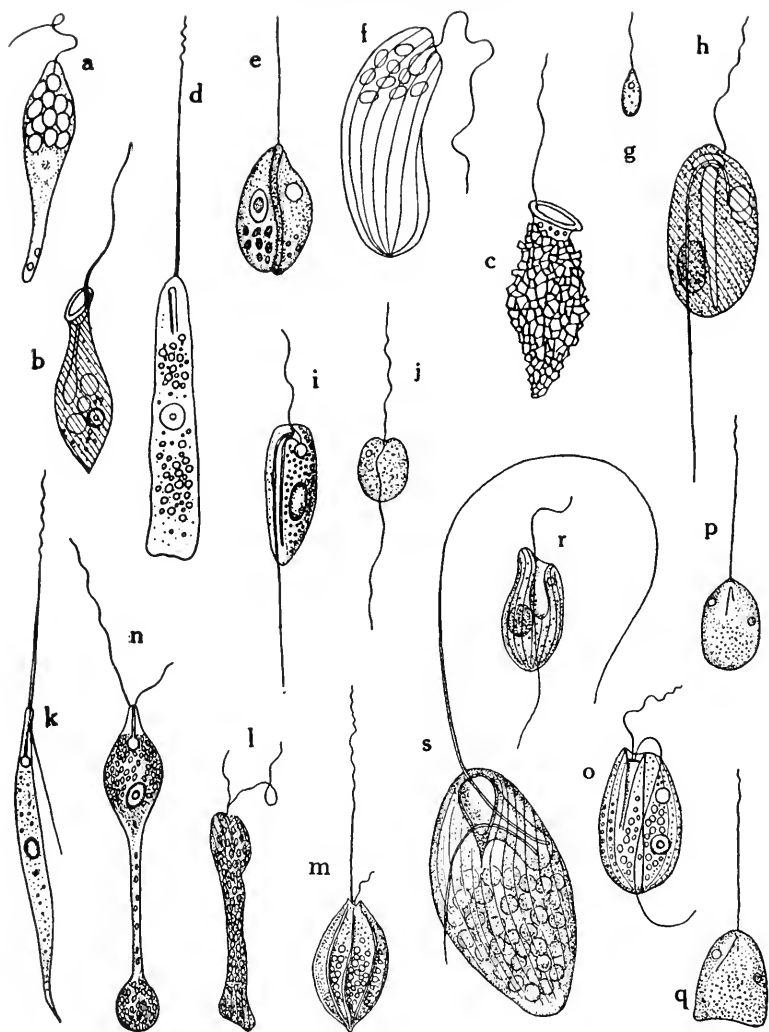


FIG. 97. a, *Astasia klebsi*, $\times 500$ (Klebs); b, *Urceolus cyclostomus*, $\times 430$ (Stein); c, *U. sabulosus*, $\times 430$ (Stokes); d, *Peranema trichophorum*, $\times 530$ (Kudo); e, *Petalmonas mediocancellata*, $\times 1000$ (Klebs); f, *Menoidium incurvum*, $\times 1400$ (Hall); g, *Scytomonas pusilla*, $\times 430$ (Stein); h, *Anisonema acinus*, $\times 400$ (Klebs); i, *A. truncatum*, $\times 430$ (Stein); j, *A. emarginatum*, $\times 530$ (Stokes); k, *Heteronema acus*, $\times 430$ (Stein); l, *H. mutabile*, $\times 120$ (Stokes); m, *Tropidoscyphus octocostatus*, $\times 290$ (Lemmermann); n, *Distigma proteus*, $\times 430$ (Stein); o, *Eutosiphon sulcatum*, $\times 430$ (Stein); p, *Notosolenus apocamptus*, $\times 1200$ (Stokes); q, *N. sinatus*, $\times 600$ (Stokes); r, *Marsupiogaster striata*, $\times 590$ (Schewiakoff); s, *M. picta* (Faria, da Cunha and Pinto).

usually an elongated form; there is a cytopharynx and cytostome, the former being connected with the reservoir of contractile vacuoles; without stigma; flagellum usually straight and its free end vibrates in a characteristic manner; asexual reproduction by longitudinal fission.

Genus **Astasia** Dujardin. Body plastic, although ordinarily elongate; fresh water or endoparasitic (?) in Cyclops, etc. Several species.

A. klebsi Lemmermann (Fig. 97, *a*). Spindle-form; posterior portion drawn out; flagellum as long as body; plastic; paramylon bodies oval; $50-60\mu$ by $13-20\mu$; stagnant water.

Genus **Urceolus** Mereschkowsky (*Phialonema* Stein). Body colorless; plastic; flask-shaped; striated; a funnel-like neck; posterior region stout; a single flagellum protrudes from funnel and reaches inward the posterior third of body; fresh or salt water.

U. cyclostomus (Stein) (Figs. 8, *f*; 97, *b*). $25-50\mu$ long; fresh water.

U. sabulosus (Stokes) (Fig. 97, *c*). Spindle-form; surface covered with minute sand-grains; about 58μ long; fresh water.

Genus **Peranema** Dujardin. Elongate with a broad, rounded or truncate posterior end during locomotion; highly plastic when stationary; delicate pellicle shows a fine striation; flagellum long, tapers toward free end and vibrates; nucleus central; contractile vacuoles; saprozoic and holozoic; in stagnant water; often in hay infusion.

P. trichophorum (Ehrenberg) (Figs. 26; 97, *d*). $20-70\mu$ long; very common.

P. granulifera Penard. Much smaller, $8-15\mu$ long; spherical or elongate; pellicle granulated; standing water.

Genus **Petalomonas** Stein. Colorless; constant in form; pellicle often with longitudinal keels on one side; a single flagellum; holozoic or saprozoic; cytostome at anterior end; cytopharynx fairly deep; in fresh water, rich in vegetable matter. Many species.

P. mediocanellata S. (Fig. 97, *e*). Ovoid with longitudinal furrow; flagellum about as long as body; $22-23\mu$ long.

Genus **Menoidium** Perty. Rigid body, more or less curved; pellicle striated; a single flagellum; fresh water.

M. incurvum (Fresenius) (Figs. 24, *d*; 64; 97, *f*). Crescentic cyl-

inder; flagellum as long as body; nucleus central or terminal; 15–25 μ by 7–8 μ ; in standing fresh water. Hall (1923) made a careful cytological study of the organism.

M. tortuosum Stokes. S-form; posterior end drawn out to a sharp point; elongate paramylon bodies; 42–78 μ long; in infusion.

Genus **Scytomonas** Stein. Oval or pyriform, with a delicate pellicle; a single flagellum; a contractile vacuole with a reservoir; holozoic on bacteria; longitudinal fission in motile stage; stagnant water and coprozoic.

S. pusilla S. (Fig. 97, *g*). About 15 μ long.

Genus **Copromonas** Dobell. Elongate ovoid; with a single flagellum; a small cytostome at anterior end; holozoic on bacteria; permanent fusion followed by encystment (p. 145); coprozoic in faecal matters of frog, toad, and man; several authors hold that this genus is probably identical with *Scytomonas* which was incompletely described by Stein.

C. subtilis D. (Fig. 69). 7–20 μ long.

Family 3 **Anisonemidae** Schewiakoff

Colorless body plastic or rigid with a variously marked pellicle; 2 flagella, one directed anteriorly and the other usually posteriorly; contractile vacuoles and reservoir; stigma absent; paramylon bodies as a rule present; free-swimming or creeping.

Genus **Anisonema** Dujardin. Generally ovoid; more or less flattened; asymmetrical; plastic or rigid; a slit-like ventral furrow; flagella at anterior end; cytopharynx long; contractile vacuole anterior; nucleus posterior; in fresh water. Several species.

A. acinus D. (Fig. 97, *h*). Rigid; oval; somewhat flattened; pellicle slightly striated; 25–40 μ by 16–22 μ .

A. truncatum Stein (Fig. 97, *i*). Rigid; ovoid; 60 μ by 20 μ .

A. emarginatum Stokes (Fig. 97, *j*). Rigid; 14 μ long; flagella long.

Genus **Heteronema** Dujardin. Plastic; rounded or elongate; flagella arise from anterior end, one directed forward and the other trailing; cytostome near base of flagella; holozoic; fresh water. Several species.

H. acus (Ehrenberg) (Fig. 97, *k*). Extended body tapers towards both ends; anterior flagellum as long as body, trailing one about 1/2; contractile vacuole anterior; nucleus central; 45–50 μ long; fresh water.

H. mutabile (Stokes) (Fig. 97, *l*). Elongate; highly plastic; longitudinally striated; about 254μ long; in cypress swamp.

Genus **Tropidoscyphus** Stein. Slightly plastic; pellicle with 8 longitudinal ridges; 2 unequal flagella at anterior pole; holozoic or saprozoic; fresh or salt water.

T. octocostatus S. (Fig. 97, *m*). $35\text{--}63\mu$ long; fresh water, rich in vegetation.

Genus **Distigma** Ehrenberg. Plastic; elongate when extended; body surface without any marking; 2 flagella unequal in length, directed forward; cytostome and cytopharynx located at anterior end; endoplasm transparent; holozoic. One species.

D. proteus E. (Fig. 97, *n*). $50\text{--}110\mu$ long when extended; nucleus central; stagnant water; infusion.

Genus **Entosiphon** Stein. Oval, flattened; more or less rigid; flagella arise from a cytostome, one flagellum trailing; protrusible cytopharynx a long conical tubule almost reaching posterior end; nucleus centro-lateral; fresh water.

E. sulcatum (Dujardin) (Fig. 97, *o*). About 20μ long.

E. ovatum Stokes. Anterior end rounded; 10–12 longitudinal striae; about $25\text{--}28\mu$ long.

Genus **Notosolenus** Stokes. Free-swimming; rigid oval; ventral surface convex, dorsal surface with a broad longitudinal groove; flagella anterior; one long, directed anteriorly and vibratile; the other shorter and trailing; fresh water with vegetation.

N. apocamptus S. (Fig. 97, *p*). Oval with broad posterior end; $6\text{--}11\mu$ long.

N. sinuatus S. (Fig. 97, *q*). Posterior end truncate or concave; about 22μ long.

Genus **Marsupiogaster** Schewiakoff. Oval; flattened; asymmetrical; cytostome occupies entire anterior end; cytopharynx conspicuous, $1/2$ body length; body longitudinally striated; 2 flagella, one directed anteriorly, the other posteriorly; spherical nucleus; contractile vacuole anterior; fresh or salt water.

M. striata Schewiakoff (Fig. 97, *r*). About 27μ by 15μ ; fresh water; Hawaii.

M. picta Faria, da Cunha et Pinto (Fig. 97, *s*). In salt water; Rio de Janeiro.

Order 5 Chloromonadina Klebs

The chloromonads are of rare occurrence and consequently not

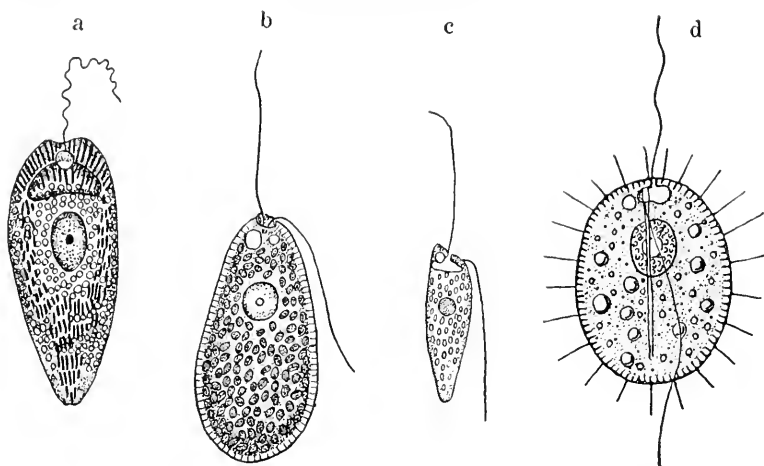


FIG. 98. a, *Gonyostomum semen*, $\times 540$ (Stein); b, *Vacuolaria virescens*, $\times 460$ (Senn); c, *Trentonia flagellata*, $\times 330$ (Stokes); d, *Thaumatomastix setifera*, $\times 830$ (Lauterborn).

well known. The majority possess small discoidal grass-green chromatophores with a large amount of xanthophyll which on addition of an acid become blue-green. No pyrenoids occur. The metabolic products are fatty oil. Starch or allied carbohydrates are absent. Stigma is also not present.

Genus **Gonyostomum** Diesing (*Rhaphidomonas* Stein). With grass-green chromatophores; highly refractile trichocyst-like structures in cytoplasm; in fresh water. A few species.

G. semen D. (Fig. 98, a). Sluggish animal; about $45\text{--}60\mu$ long; in marshy water among decaying vegetation.

Genus **Vacuolaria** Cienkowski. Highly plastic; without trichocyst-like structures; anterior end narrow; with 2 flagella; cysts with a gelatinous envelope. One species.

V. virescens C. (Fig. 98, b). About $50\text{--}150\mu$ long; fresh water.

Genus **Trentonia** Stokes. Bi-flagellate as in the last genus; but flattened; anterior margin slightly bilobed. One species.

T. flagellata S. (Fig. 98, c). Slow-moving organism; encystment followed by binary fission; about 60μ long; fresh water.

Genus **Thaumatomastix** Lauterborn. Colorless; pseudopodia formed; 2 flagella, one extended anteriorly, the other trailing; holozoic; perhaps a transitional form between the Mastigophora and the Sarcodina. One species.

T. setifera L. (Fig. 98, d). About $20\text{--}35\mu$ by $15\text{--}28\mu$; fresh water.

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CHAPTER 11

Order 6 Dinoflagellata Bütschli

THE dinoflagellates make one of the most distinct groups of the Mastigophora, inhabiting mostly marine water, and to a lesser extent fresh water. In the general appearance, the arrangement of the two flagella, the characteristic furrows, and the possession of brown chromatophores, they are closely related to the Cryptomonadina.

The body is covered by an envelope composed of cellulose which may be a simple smooth piece, or may be composed of two valves or of numerous plates, that are variously sculptured and possess manifold projections. Differences in the position and course of the furrows and in the projections of the envelope produce numerous asymmetrical forms. The furrows, or grooves, are a transverse annulus and a longitudinal sulcus. The **annulus** is a girdle around the middle or toward one end of the body. It may be a complete or incomplete ring or sometimes spiral. While the majority show a single transverse furrow, a few may possess several. The part of the shell anterior to the annulus is called the **epitheca** and that posterior to the annulus the **hypothecca**. In case the envelope is not developed, the terms **epicone** and **hypocone** are used (Fig. 99). The **sulcus** may run from end to end or from one end to the annulus. The two flagella arise typically from the annulus, one being transverse and the other longitudinal.

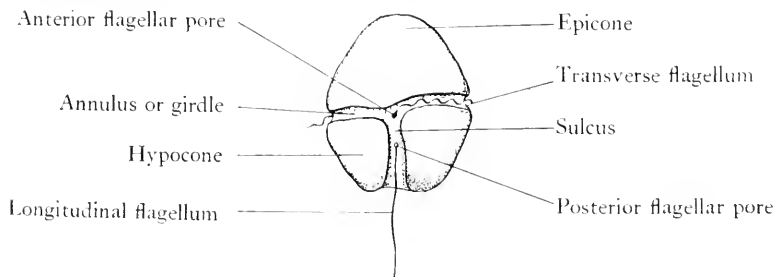


FIG. 99. Diagram of a typical naked dinoflagellate (Lebour).

The **transverse flagellum** which is often band-form, encircles the body and undergoes undulating movements, which in former

years were looked upon as ciliary movements (hence the name Cilioflagellata). In the suborder Adinida, this flagellum vibrates freely in a circle near the anterior end. The **longitudinal flagellum** often projects beyond the body and vibrates. Combination of the movements of these flagella produces whirling movements characteristic of the organisms.

The majority of dinoflagellates possess a single somewhat massive nucleus with evenly scattered chromatin, and usually several endosomes. There are two kinds of vacuoles. One is often surrounded by a ring of smaller vacuoles, while the other is large contains pink-colored fluid and connected with the exterior by a canal opening in a flagellar pore. The latter is known as the **pusule** which functions as a digestive organella (Kofoed and Swezy). In many freshwater forms a stigma is present, and in Pouchetiidae there is an ocellus composed of an amyloid lens and a dark pigment-ball. The majority of planktonic forms possess a large number of small chromatophores which are usually dark yellow, brown or sometimes slightly greenish and are located in the periphery of the body, while bottom-dwelling and parasitic forms are, as a rule, colorless, because of the absence of chromatophores. A few forms contain haematochrome. The method of nutrition is holophytic, holozoic, saprozoic, or mixotrophic. In holophytic forms, anabolic products are starch, oil, or fats.

Asexual reproduction is by binary or multiple fission or budding in either the active or the resting stage and differs among different groups. Encystment is of common occurrence. In some forms the cyst wall is formed within the test. The cysts remain alive for many years; for example, *Ceratium* cysts were found to retain their vitality in one instance for six and one-half years. Conjugation and sexual fusion have been reported in certain forms, but definite knowledge on sexual reproduction awaits further investigation.

The dinoflagellates are abundant in the plankton of the sea and play an important part in the economy of marine life as a whole. A number of parasitic forms are also known. Their hosts include various diatoms, copepods and several pelagic animals.

- Bivalve shell without furrows....Suborder 1 Prorocentrinea (p. 218)
- Nakes or with shell showing furrows.....
-Suborder 2 Peridiniinea (p. 219)
- Naked; without furrows; no transverse flagellum.....
-Suborder 3 Cystoflagellata (p. 233)

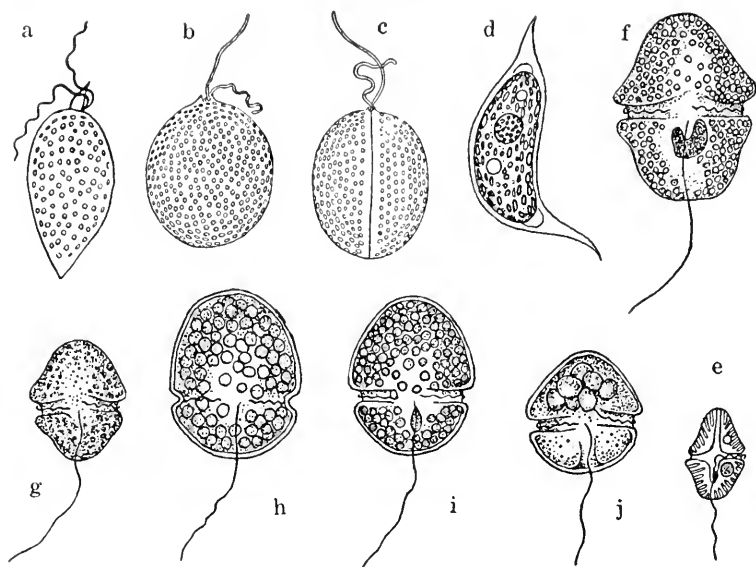


FIG. 100. a, *Prorocentrum micans*, $\times 420$ (Schütt); b, c, *Exuviaella marina*, $\times 420$ (Schütt); d, e, *Cystodinium steini*, $\times 370$ (Klebs); f, *Glenodinium cinctum*, $\times 590$ (Schilling); g, *G. pulvisculum*, $\times 420$ (Schilling); h, *G. uliginosum*, $\times 590$ (Schilling); i, *G. edax*, $\times 490$ (Schilling); j, *G. neglectum*, $\times 650$ (Schilling).

Suborder 1 **Prorocentrinea** Poche

Test bivalve; without any groove; with yellow chromatophores; 2 flagella anterior, one directed anteriorly, the other vibrates in a circle; fresh or salt water.

Family **Prorocentridae** Kofoid

Genus **Prorocentrum** Ehrenberg. Elongate oval; anterior one bluntly pointed, with a spinous projection at pole; chromatophores small, yellowish brown; salt water.

P. micans E. (Fig. 100, a). $36\text{--}52\mu$ long; a cause of "red water."

P. triangulatum Martin. Triangular with rounded posterior end; shell-valves flattened; one valve with a delicate tooth; surface covered with minute poroids; margin striated; chromatophores yellow-brown, irregular, broken up in small masses; $17\text{--}22\mu$ (excluding tooth); Martin found it extremely abundant in brackish water in New Jersey.

Genus **Exuviaella** Cienkowski. Subspherical or oval; no anterior projection, except 2 flagella; 2 lateral chromatophores, large, brown, each with a pyrenoid and a starch body; nucleus posterior; salt water. Several species.

E. marina C. (Fig. 100, *b*, *c*). 36–50 μ long.

E. apora Schiller. Compressed, oval; striae on margin of valves; chromatophores numerous yellow-brown irregular in form; 30–32 μ by 21–26 μ (Schiller); 17–22 μ by 14–19; (Lebour; Martin); common in brackish water, New Jersey.

Suborder 2 **Peridiniinea** Poche

Typical dinoflagellates with one to many transverse annuli and a sulcus; 2 flagella, one of which undergoes a typical undulating movement, while the other usually directed posteriorly. According to Kofoed and Swezy, this suborder is divided into two tribes. Body naked or covered by a thin shell . . . Tribe 1 Gymnodinioidae
Body covered by a thick shell Tribe 2 Peridinioidae
(p. 229)

Tribe 1 **Gymnodinioidae** Poche

Naked or covered by a single piece cellulose membrane with annulus and sulcus, and 2 flagella; chromatophores abundant, yellow or greenish platelets or bands; stigma sometimes present; asexual reproduction binary or multiple division; holophytic, holozoic, or saprozoic; the majority are deep-sea forms; a few coastal or fresh water forms also occur.

With a cellulose membrane Family 1 Cystodiniidae
Without shell

Furrows rudimentary Family 2 Pronoctilucidae (p. 220)

Annulus and sulcus distinct

Solitary

With ocellus Family 3 Pouchetiidae (p. 220)

Without ocellus

With tentacles Family 4 Noctilucidae (p. 222)

Without tentacles

Free-living Family 5 Gymnodiniidae (p. 223)

Parasitic Family 6 Blastodiniidae (p. 227)

Permanently colonial Family 7 Polykrikidae (p. 228)

Family 1 **Cystodiniidae** Kofoed et Swezy

Genus **Cystodinium** Klebs. In swimming phase, oval, with ex-

tremely delicate envelope; annulus somewhat acyclic; cyst-membrane drawn out into 2 horns.

C. steini K. (Fig. 100, *d, e*). Stigma beneath sulcus; chromatophores brown; swarmer about 45μ long; freshwater ponds.

Genus **Glenodinium** Ehrenberg. (*Glenodiniopsis*, *Staszicella*, Woloszynska). Spherical; ellipsoidal or reniform in end-view; annulus a circle; several discoidal, yellow to brown chromatophores; horseshoe- or rod-shaped stigma in some; often with gelatinous envelope; fresh water. Many species.

G. cinctum E. (Fig. 100, *f*). Spherical to ovoid; annulus equatorial; stigma horseshoe-shaped; 43μ by 40μ .

G. pulvisculum Stein (Fig. 100, *g*). No stigma; 38μ by 30μ .

G. uliginosum Schilling (Fig. 100, *h*). $36\text{--}48\mu$ by 30μ .

G. edax S. (Fig. 100, *i*). 34μ by 33μ .

G. neglectum S. (Fig. 100, *j*). $30\text{--}32\mu$ by 29μ .

Family 2 **Pronoctilucidae** Lebour

Genus **Pronoctiluca** Fabre-Domergue. Body with an anteroventral tentacle and sulcus; annulus poorly marked; salt water.

P. tentaculatum (Kofoid et Swezy) (Fig. 101, *a*). About 54μ long; off California.

Genus **Oxyrrhis** Dujardin. Subovoidal, asymmetrical posteriorly; annulus incomplete; salt water.

O. marina D. (Fig. 101, *b*). $10\text{--}37\mu$ long.

Family 3 **Pouchetiidae** Kofoid et Swezy

Ocellus consists of lens and melanosome (pigment mass); sulcus and annulus somewhat twisted; pusules usually present; cytoplasm colored; salt water (pelagic).

Genus **Pouchetia** Schütt. Nucleus anterior to ocellus; ocellus with red or black pigment mass with a red, brown, yellow, or colorless central core; lens hyaline; body surface usually smooth; holozoic; encystment common; salt water. Many species.

P. fusus S. (Fig. 101, *c*). About 94μ by 41μ ; ocellus 27μ long.

P. maxima Kofoid et Swezy (Fig. 101, *d*). 145μ by 92μ ; ocellus 20μ ; off California.

Genus **Protopsis** Kofoid et Swezy. Annulus and sulcus similar to those of *Gymnodinium* or *Gyrodinium*; with a simple or compound ocellus, no tentacles; body not twisted; salt water. A few species.

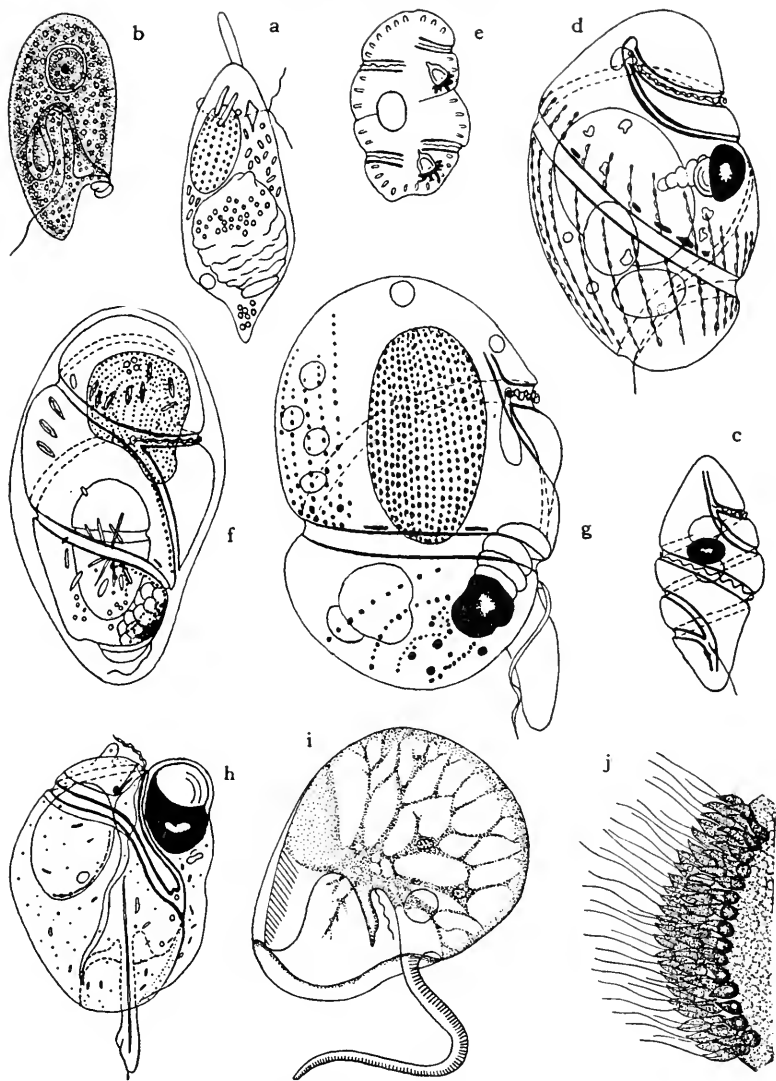


FIG. 101. a, *Pronoctiluca tentaculatum*, $\times 730$ (Kofoid and Swezy); b, *Oxyrrhis marina*, $\times 840$ (Senn); c, *Pouchetia fusus*, $\times 340$ (Schütt); d, *P. maxima*, $\times 330$ (Kofoid and Swezy); e, *Protopsis ochrea*, $\times 340$ (Wright); f, *Nematodinium partitum*, $\times 560$ (Kofoid and Swezy); g, *Proterythropsis crassicaudata*, $\times 740$ (Kofoid and Swezy); h, *Erythropsis cornuta*, $\times 340$ (Kofoid and Swezy); i, j, *Noctiluca scintillans* (i. side view; j, budding process), $\times 140$ (Robin).

P. ochrea (Wright) (Fig. 101, *e*). 55μ by 45μ ; ocellus 22μ long; Nova Scotia.

Genus **Nematodinium** Kofoid et Swezy. With nematocysts; girdle more than 1 turn; ocellus distributed or concentrated, posterior; holozoic; salt water.

N. partitum K. et S. (Fig. 101, *f*). 91μ long; off California.

Genus **Proterythropsis** Kofoid et Swezy. Annulus median; ocellus posterior; a stout rudimentary tentacle or prod-like antapical process; salt water. One species.

P. crassicaudata K. et S. (Fig. 101, *g*). 70μ long; off California.

Genus **Erythropsis** Hertwig. Epicone flattened, less than $1/4$ hypocone; ocellus very large, composed of one or several hyaline lenses attached to or imbedded in a red, brownish or black pigment body with a red, brown or yellow core, located at left of sulcus; sulcus expands posteriorly into ventro-posterior tentacle; salt water. Several species.

E. cornuta (Schütt) (Fig. 101, *h*). 104μ long; off California (Kofoid and Swezy).

Family 4 Noctilucidae Kent

Tentacle somewhat contractile, arises from sulcal area and extends posteriorly; this group had formerly been included in the Cystoflagellata; studies by recent investigators, particularly by Kofoid, show their affinities with the present suborder; holozoic; salt water.

Genus **Noctiluca** Suriray. Spherical, bilaterally symmetrical; peristome marks median line of body; a cytostome at bottom of peristome; with a conspicuous tentacle; cytoplasm much vacuolated, and cytoplasmic strands connect central mass with periphery; peripheral granules phosphorescent (p. 95); cytoplasm colorless or blue-green; sometimes tinged with yellow coloration in center; swimmers formed by budding, and each possesses one flagellum, annulus, and tentacle; widely distributed in salt water; holozoic. One species.

N. scintillans (Macartney) (*N. miliaris* S.) (Fig. 101, *i, j*). Usually 500 – 1000μ in diameter, with extremes of 200μ and 2 mm. Gross (1934) observed that complete fusion of two swimmers (isogametes) results in cyst formation from which trophozoites develop. Acid contents of the body fluid is said to be about pH 3.

Genus **Pavillardia** Kofoid et Swezy. Annulus and sulcus similar to those of *Gymnodinium*; longitudinal flagellum absent; stout

finger-like mobile tentacle directed posteriorly; salt water. One species.

P. tentaculifera K. et S. 58μ by 27μ ; pale yellow; off California.

Family 5 **Gymnodiniidae** Kofoid

Naked forms with simple but distinct $1/2$ –4 turns of annulus; with or without chromatophores; fresh or salt water.

Genus **Gymnodinium** Stein. Pellicle delicate; subcircular; bilaterally symmetrical; numerous discoid chromatophores varicolored (yellow to deep brown, green, or blue) or sometimes absent; stigma present in few; many with mucilaginous envelope; salt, brackish, or fresh water. Numerous species.

G. aeruginosum S. (Fig. 102, a). Chromatophores green; 33 – 35μ by 22μ ; ponds and lakes.

G. rotundatum Klebs (Fig. 102, b). 32 – 35μ by 22 – 25μ ; fresh water.

G. palustre Schilling (Fig. 102, c). 45μ by 38μ ; fresh water.

G. agile Kofoid et Swezy (Fig. 102, d). About 28μ long; in sandy beaches.

Genus **Hemidinium** Stein. Asymmetrical; oval; annulus about half a turn, only on left half. One species.

H. nasutum S. (Fig. 102, e). Sulcus on hypocone; chromatophores yellow to brown; with a reddish brown oil drop; nucleus posterior; transverse fission; 24 – 28μ by 16 – 17μ ; fresh water.

Genus **Amphidinium** Claparède et Lachmann. Form variable; epicone small; annulus anterior; sulcus straight on hypocone or also on part of epicone; with or without chromatophores; mainly holophytic, some holozoic; coastal or fresh water. Numerous species.

A. lacustre Stein (Fig. 102, f). 30μ by 18μ ; in fresh and salt (?) water.

A. scissum Kofoid et Swezy (Fig. 102, g). 50 – 60μ long; in sandy beaches.

A. fusiforme Martin. Fusiform, twice as long as broad; circular in cross-section; epicone rounded conical; annulus anterior; hypocone 2–2.5 times as long as epicone; sulcus obscure; body filled with yellowish green chromatophores except at posterior end; stigma dull orange, below girdle; nucleus ellipsoid, posterior to annulus; pellicle delicate; 17 – 22μ by 8 – 11μ in diameter. Martin (1929) found that it was extremely abundant in parts of Delaware

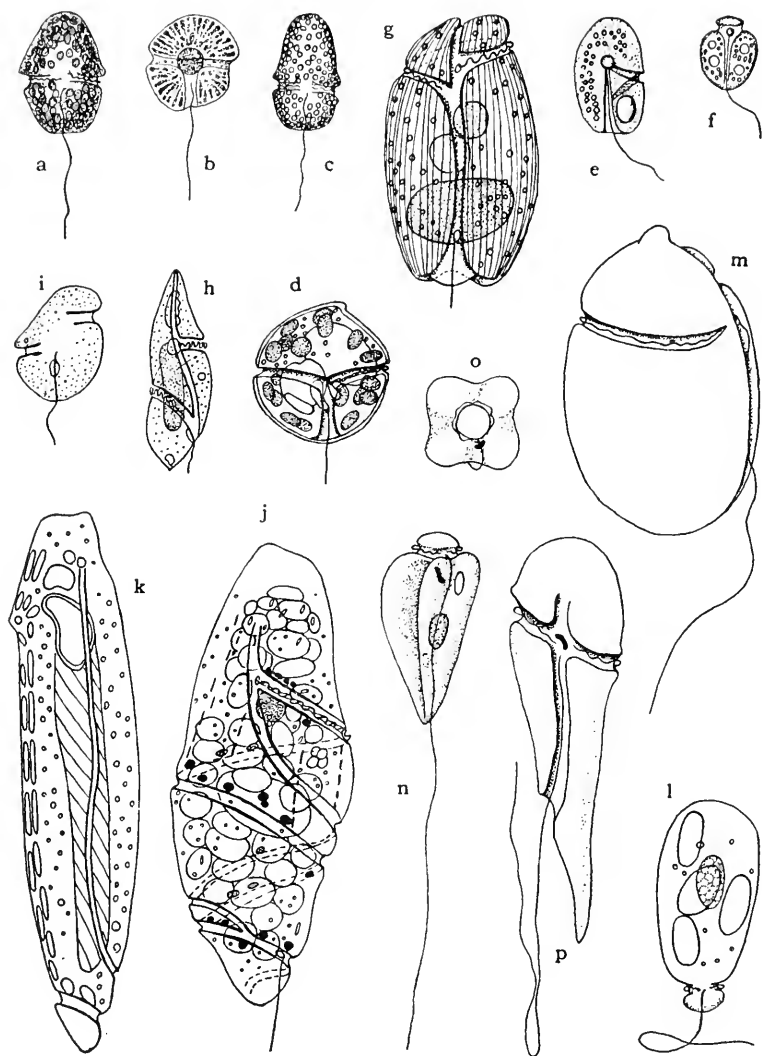


FIG. 102. a, *Gymnodinium aeruginosum*, $\times 500$ (Schilling); b, *G. rotundatum*, $\times 360$ (Klebs); c, *G. palustre*, $\times 360$ (Schilling); d, *G. agile*, $\times 740$ (Kofoid and Swezy); e, *Hemidinium nasutum*, $\times 670$ (Stein); f, *Amphidinium lacustre*, $\times 440$ (Stein); g, *A. scissum*, $\times 880$ (Kofoid and Swezy); h, *Gyrodinium biconicum*, $\times 340$ (Kofoid and Swezy); i, *G. hyalinum*, $\times 670$ (Kofoid and Swezy); j, *Cochlodinium atromaculatum*, $\times 340$ (Kofoid and Swezy); k, *Torodinium robustum*, $\times 670$ (Kofoid and Swezy); l, *Massartia nieuportensis*, $\times 670$ (Conrad); m, *Chilodinium cruciatum*, $\times 900$ (Conrad); n, o, *Trochodinium prismatium*, $\times 1270$ (Conrad); p, *Ceratodinium asymmetricum*, $\times 670$ (Conrad).

Bay and gave rise to red coloration of the water ("Red water").

Genus **Gyrodinium** Kofoid et Swezy. Annulus descending left spiral; sulcus extending from end to end; nucleus central; pusules; surface smooth or striated; chromatophores rarely present; cytoplasm colored; holozoic; salt or fresh water. Many species.

G. biconicum K. et S. (Fig. 102, *h*). 68μ long; salt water; off California.

G. hyalinum (Schilling) (Fig. 102, *i*). About 24μ long; freshwater.

Genus **Cochlodinium** Schütt. Twisted at least 1.5 turns; annulus descending left spiral; pusules; cytoplasm colorless to highly colored; chromatophores rarely present; holozoic; surface smooth or striate; salt water. Numerous species.

C. atromaculatum Kofoid et Swezy (Fig. 102, *j*). $183\text{--}185\mu$ by 72μ ; longitudinal flagellum 45μ long; off California.

Genus **Torodinium** Kofoid et Swezy. Elongate; epicone several times longer than hypocone; annulus and hypocone form augur-shaped cone; sulcus long; nucleus greatly elongate; salt water. 2 species.

T. robustum K. et S. (Fig. 102, *k*). $67\text{--}75\mu$ long; off California.

Genus **Massartia** Conrad. Cylindrical; epicone larger (9–10 times longer and 3 times wider) than hypocone; no sulcus; with or without yellowish discoid chromatophore.

M. nieuportensis C. (Fig. 102, *l*). $28\text{--}37\mu$ long; brackish water.

Genus **Chilodinium** Conrad. Ellipsoid; posterior end broadly rounded, anterior end narrowed and drawn out into a digitiform process closely adhering to body; sulcus, apex to $1/5$ from posterior end; annulus oblique, in anterior $1/3$.

C. cruciatum C. (Fig. 103, *m*). $40\text{--}50\mu$ by $30\text{--}40\mu$; with trichocysts; brackish water.

Genus **Trochodinium** Conrad. Somewhat similar to *Amphidinium*; epicone small, button-like; hypocone with 4 longitudinal rounded ridges; stigma; without chromatophores.

T. prismaticum C. (Fig. 102, *n*, *o*). $18\text{--}22\mu$ by $9\text{--}12\mu$; epicone $5\text{--}7\mu$ in diameter; brackish water.

Genus **Ceratodinium** Conrad. Cuneiform; asymmetrical, colorless, more or less flattened; annulus complete, oblique; sulcus on half of epicone and full length of hypocone; stigma.

C. asymmetricum C. (Fig. 102, *p*). $68\text{--}80\mu$ by about 10μ ; brackish water.

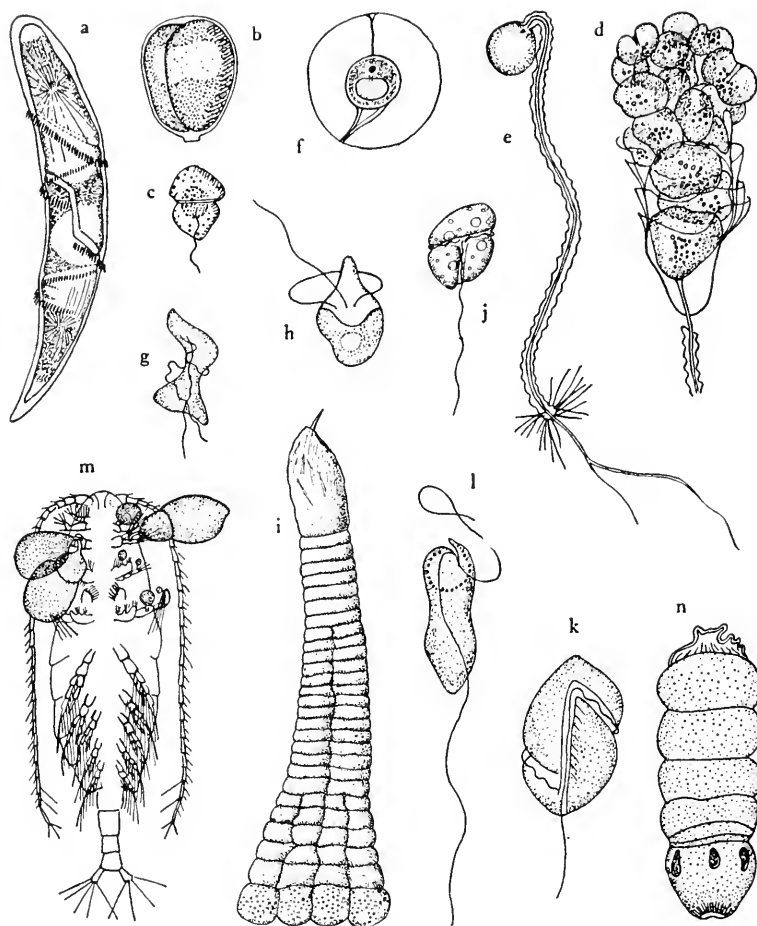


FIG. 103. a, *Blastodinium spinulosum*, $\times 240$ (Chatton); b, c, *Oodinium poucheti* (c, a swarmer) (Chatton); d, e, *Apodinium mycetoides* (d, swarmer-formation, $\times 450$; e, a younger stage, $\times 640$) (Chatton); f, *Chytridinium parasiticum* in a copepod egg (Dogiel); g, *Trypanodinium ovicola*, $\times 1070$ (Chatton); h, *Duboscquella tintinnicola* (Duboscq and Collin); i, j, *Haplozoon clymenellae* (i, mature colony, $\times 300$; j, a swarmer, $\times 1340$) (Shumway); k, *Syndinium turbo*, $\times 1340$ (Chatton); l, *Paradinium poucheti*, $\times 800$ (Chatton); m, *Ellobiopsis chattoni* on *Calanus finmarchicus* (Caullery); n, *Paraellobiopsis couticri* (Collin).

Family 6 **Blastodiniidae** Kofoid et Swezy

All parasitic in or on plants and animals; in colony forming genera, there occur **trophocyte** (Chatton) by which organism is attached to host and more or less numerous **gonocytes** (Chatton).

Genus **Blastodinium** Chatton. In gut of copepods; spindle-shaped, arched, ends attenuated; envelope (not cellulose) often with 2 spiral rows of bristles; young forms binucleate; when present, chromatophores in yellowish brown network; swimmers similar to those of *Gymnodinium*; in salt water. Many species.

B. spinulosum C. (Fig. 103, a). About 235μ by $33\text{--}39\mu$; swimmers $5\text{--}10\mu$; in *Palacalanus parvus*, *Clausocalanus arcuicornis* and *C. furcatus*.

Genus **Oodinium** Chatton. Spherical or pyriform; with a short stalk; nucleus large; often with yellowish pigment; on Salpa, Annelida, Siphonophora, etc.

O. poucheti (Lemmermann) (Fig. 103, b, c). Fully grown individuals up to 170μ long; bright yellow ochre; mature forms become detached and float, dividing into numerous gymnodinium-like swimmers; on the tunicate, *Oikopleura dioica*.

Genus **Apodinium** Chatton. Young individuals elongate, spherical or pyriform; binucleate; adult colorless; formation of numerous swimmers in adult stage is peculiar in that lower of the 2 individuals formed at each division secretes a new envelope, and delays its further division until the upper divides for the second time, leaving several open cups; on tunicates.

A. mycetoides C. (Fig. 103, d, e). On gill-slits of *Fritillaria pelucida*.

Genus **Chytriodinium** Chatton. In eggs of planktonic copepods; young individuals grow at the expense of host egg and when fully formed, body divides into many parts, each producing 4 swimmers. Several species.

C. parasiticum (Dogiel) (Fig. 103, f). In copepod eggs; Naples.

Genus **Trypanodinium** Chatton. In copepod eggs; swimmer-stage only known.

T. ovicola C. (Fig. 103, g). Swimmers biflagellate; about 15μ long.

Genus **Duboscquella** Chatton. Rounded cell with a large nucleus; parasitic in Tintinnidiidae. One species.

D. tintinnicola (Lohmann) (Fig. 103, h). Intracellular stage oval, about 100μ in diameter with a large nucleus; swimmers biflagellate.

Genus **Haplozoon** Dogiel. In gut of polychaetes; mature forms composed of variable number of cells arranged in line or in pyramid; salt water. Many species.

H. clymenellae (Calkins) (Fig. 103, *i, j*). In *Clymenella torquata*; colonial forms consist of 250 or more cells; Woods Hole.

Genus **Syndinium** Chatton. In gut and body cavity of marine copepods; multinucleate round cysts in gut considered as young forms; multinucleate body in host body cavity with numerous needle-like inclusions.

S. turbo C. (Fig. 103, *k*). In *Paracalanus parvus*, *Corycaeus venustus*, *Calanus finmarchicus*; swarmers about 15μ long.

Genus **Paradinium** Chatton. In body-cavity of copepods; multinucleate body without inclusions; swarmers formed outside the host body.

P. poucheti C. (Fig. 103, *l*). In the copepod, *Acartia clausi*; swarmers about 25μ long, amoeboid.

Genus **Ellobiopsis** Caullery. Pyriform; with stalk; often a septum near stalked end; attached to anterior appendages of marine copepods.

E. chattoni C. (Fig. 103, *m*). Up to 700μ long; on antennae and oral appendages of *Calanus finmarchicus*, *Pseudocalanus elongatus* and *Acartia clausi*.

Genus **Paraellobiopsis** Collin. Young forms stalkless; spherical; mature individuals in chain-form; on Malacostraca.

P. coutieri C. (Fig. 103, *n*). On appendages of *Nebalia bipes*.

Family 7 Polykrikidae Kofoid et Swezy

2, 4, 8, or 16 individuals permanently joined in chain; individuals similar to *Gymnodinium*; sulcus however extending entire body length; with nematocysts (Fig. 104, *b*); greenish to pink; nuclei about $1/2$ the number of individuals; holozoic; salt water.

Genus **Polykrikos** Bütschli. With the above-mentioned characters; salt or brackish water.

P. kofoidi (Chatton) (Fig. 104, *a, b*). Greenish grey to rose; composed of 2, 4, 8, or 16 individuals; with nematocysts; each nematocyst possesses presumably a hollow thread, and discharged under suitable stimulation; a binucleate colony composed of 4 individuals about 110μ long; off California.

P. barnegatensis Martin. Ovate, nearly circular in cross-section, slightly concave ventrally; composed of 2 individuals; constrict-

tion slight; beaded nucleus in center; annuli descending left spiral, displaced twice their width; sulcus ends near anterior end; cytoplasm colorless, with numerous oval, yellow-brown chromatophores; nematocysts absent; 46μ by 31.5μ ; in brackish water of Barnegat Bay.

Tribe 2 **Peridinioidae** Poche

The shell composed of epitheca, annulus and hypotheca, which may be divided into numerous plates; body form variable.

With annulus and sulcus

Shell composed of plates; but no suture. Family 1 Peridiniidae

Breast plate divided by sagittal suture.
 Family 2 Dinophysidae (p. 233)

Without annulus or sulcus. Family 3 Phytodiniidae (p. 233)

Family 1 **Peridiniidae** Kent

Shell composed of numerous plates; annulus usually at equator, covered by a plate known as **cingulum**; variously sculptured and finely perforated plates vary in shape and number among different species; in many species certain plates drawn out into various processes, varying greatly in different seasons and localities even among one and the same species; these processes seem to retard descending movement of organisms from upper to lower level in water when flagellar activity ceases; chromatophores numerous, small platelets, yellow or green; some deep-sea forms without chromatophores; chain formation in some forms; mostly surface and pelagic inhabitants in fresh or salt water.

Genus **Peridinium** Ehrenberg. Subspherical to ovoid; reniform in cross-section; annulus slightly spiral with projecting rims; hypotheca often with short horns and epitheca drawn out; colorless, green, or brown; stigma usually present; cysts spherical; salt or fresh water. Numerous species.

P. tabulatum Claparède et Lachmann (Fig. 104, *c*). 48μ by 44μ ; fresh water.

P. divergens (E.) (Fig. 104, *d*). About 45μ in diameter; yellowish, salt water.

Genus **Ceratium** Schrank. Body flattened; with one anterior and 1-4 posterior horn-like processes; often large; chromatophores yellow, brown, or greenish; color variation conspicuous; fission is said to take place at night and in the early morning;

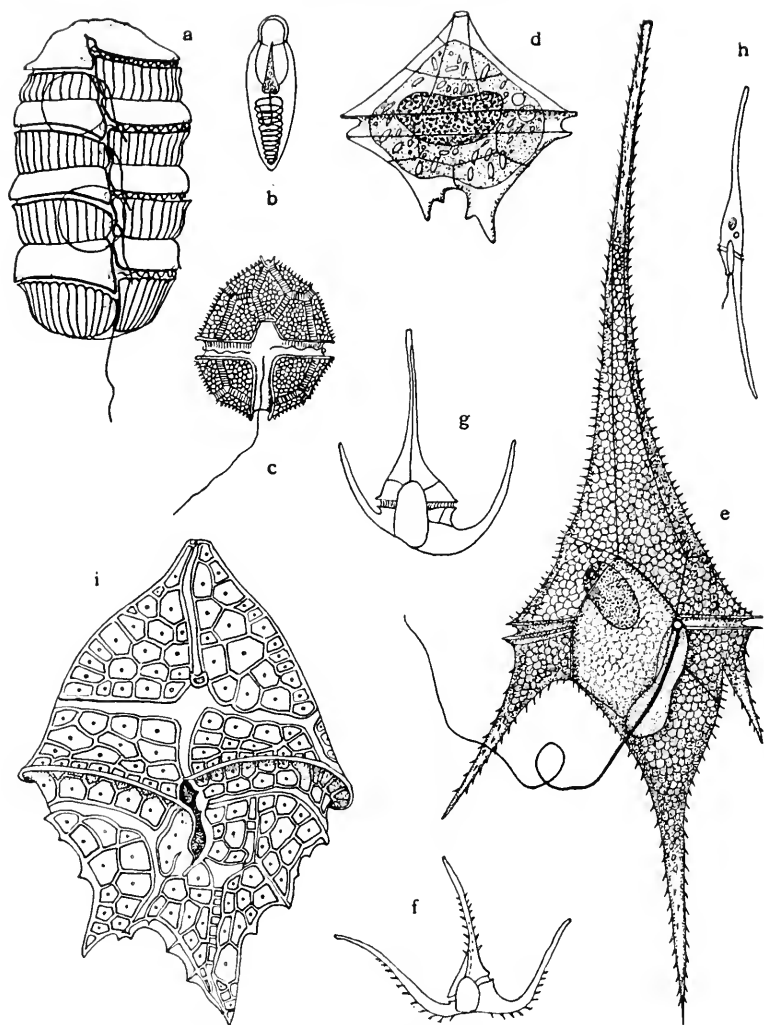


FIG. 104. a, b, *Polykrikos kofoidi* (a, colony of four individuals, $\times 340$; b, a nematocyst, $\times 1040$) (Kofoid and Swezy); c, *Peridinium tabulatum*, $\times 460$ (Schilling); d, *P. divergens*, $\times 340$ (Calkins); e, *Ceratium hirundinella*, $\times 540$ (Stein); f, *C. longipes*, $\times 100$ (Wailles); g, *C. tripos*, $\times 140$ (Wailles); h, *C. fusus*, $\times 100$ (Wailles); i, *Heterodinium scrippsi*, $\times 570$ (Kofoid and Adamson).

fresh or salt water. Numerous species; specific identification is difficult due to a great variation (p. 162).

C. hirundinella (Müller) (Figs. 80; 104, *e*). 1 apical and 2–3 antapical horns; seasonal and geographical variations; chain-formation frequent; 95–700 μ long; fresh and salt water. Numerous varieties.

C. longpipes (Bailey) (Fig. 104, *f*). About 210 μ by 51–57 μ ; salt water.

C. tripos (Müller) (Fig. 104, *g*). About 225 μ by 75 μ ; salt water. Wailes (1928) observed var. *atlantica* in British Columbia; Martin (1929) in Barnegat Inlet, New Jersey.

C. fusus (Ehrenberg) (Fig. 104, *h*). 300–600 μ by 15–30 μ ; salt water; widely distributed; British Columbia (Wailes), New Jersey (Martin), etc.

Genus **Heterodinium** Kofoid. Flattened or spheroidal; 2 large antapical horns; annulus submedian; with post-cingular ridge; sulcus short, narrow; shell hyaline, reticulate, porulate; salt water. Numerous species.

H. scippsi K. (Fig. 104, *i*). 130–155 μ long; Pacific and Atlantic (tropical).

Genus **Dolichodinium** Kofoid et Adamson. Subconical, elongate; without apical or antapical horns; sulcus not indenting epitheca; plate porulate; salt water.

D. lineatum (Kofoid et Michener) (Fig. 105, *a*). 58 μ long; eastern tropical Pacific.

Genus **Goniodoma** Stein. Polyhedral with a deep annulus; epitheca and hypotheca slightly unequal in size, composed of regularly arranged armored plates; chromatophores small brown platelets; fresh or salt water.

G. acuminata (Ehrenberg) (Fig. 105, *b*). About 50 μ long; salt water.

Genus **Gonyaulax** Diesing. Spherical, polyhedral, fusiform, or elongated with stout apical and antapical prolongations, or dorso-ventrally flattened; apex never sharply attenuated; annulus equatorial; sulcus from apex to antapex, broadened posteriorly; plates 1–6 apical, 0–3 anterior intercalaries, 6 precingulars, 6 annular plates, 6 postcingulars, 1 posterior intercalary and 1 antapical; porulate; chromatophores yellow to dark brown, often dense; without stigma; fresh, brackish or salt water. Numerous species.

G. polyedra Stein (Fig. 105, *c*). Angular, polyhedral; ridges along sutures, annulus displaced 1–2 annulus widths, regularly pitted; salt water. "Very abundant in the San Diego region in the

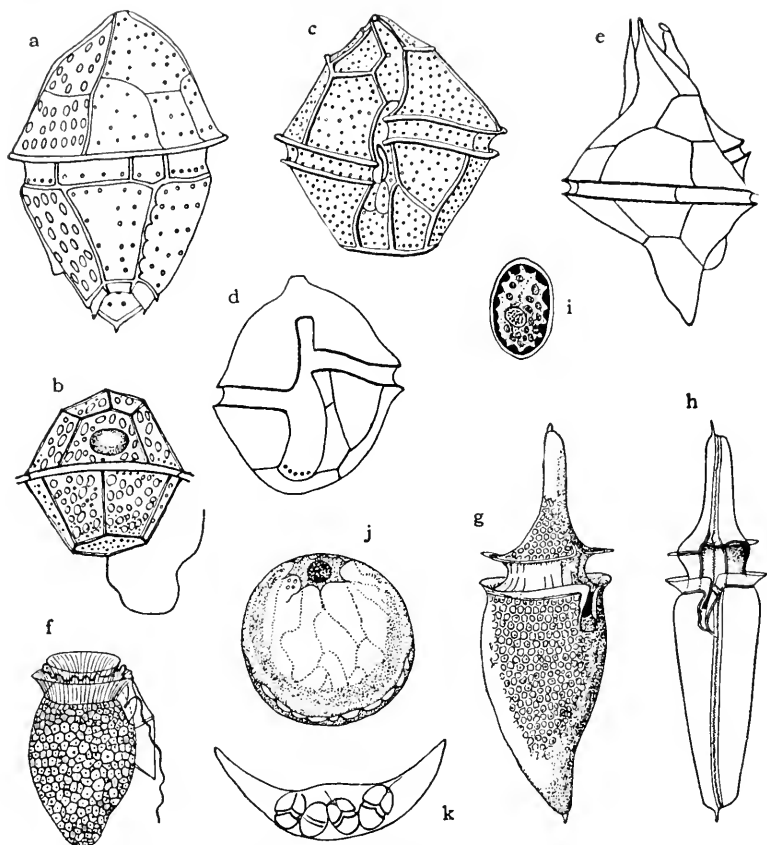


FIG. 105. a, *Dolichodinium lineatum*, $\times 670$ (Kofoid and Adamson); b, *Goniiodoma acuminata*, $\times 340$ (Stein); c, *Gonaulax polyedra*, $\times 670$ (Kofoid); d, *G. apiculata*, $\times 670$ (Lindemann); e, *Spiraulax jolliffei*, right side of theca, $\times 340$ (Kofoid); f, *Dinophysis acuta*, $\times 580$ (Schütt); g, h, *Oxyphysis oxytoroides*, $\times 780$ (Kofoid); i, *Phytodinium simplex*, $\times 340$ (Klebs); j, k, *Dissodinium lunula*: j, primary cyst (Dogiel); k, secondary cyst with 4 swarmers (Wailes), $\times 220$.

summer plankton, July–September, when it causes local outbreaks of ‘red water,’ which extend along the coast of southern and lower California” (Kofoid, 1911).

G. apiculata (Penard) (Fig. 105, d). Ovate, chromatophores yellowish brown; 30–60 μ long; fresh water.

Genus **Spiraulax** Kofoid. Biconical; apices pointed; sulcus not reaching apex; no ventral pore; surface heavily pitted; salt water.

S. jolliffei (Murray et Whitting) (Fig. 105, *e*). 132μ by 92μ ; California.

Family 2 Dinophysidae Kofoid

Genus **Dinophysis** Ehrenberg. Highly compressed; annulus widened, funnel-like, surrounding small epitheca; chromatophores yellow; salt water. Several species.

D. acuta E. (Fig. 105, *f*). Oval; attenuated posteriorly; $54\text{--}94\mu$ long; widely distributed; British Columbia (Waiiles).

Genus **Oxyphysis** Kofoid. Epitheca developed; sulcus short; sulcal lists feebly developed; sagittal suture conspicuous; annulus impressed; salt water.

O. oxytoxoides K. (Fig. 105, *g, h*). $63\text{--}68\mu$ by 15μ ; off Alaska.

Family 3 Phytodiniidae Klebs

Genus **Phytodinium** Klebs. Spherical or ellipsoidal; without furrows; chromatophores discoidal, yellowish brown.

P. simplex K. (Fig. 105, *i*). Spherical or oval; $42\text{--}50\mu$ by $30\text{--}45\mu$; fresh water.

Genus **Dissodinium** Klebs (*Pyrocystis* Paulsen). Primary cyst, spherical, uninucleate; contents divide into 8–16 crescentic secondary cysts which become set free; in them are formed 2, 4, 6, or 8 Gymnodinium-like swimmers; salt water.

D. lunula (Schütt) (Fig. 105, *j, k*). Primary cysts $80\text{--}155\mu$ in diameter; secondary cysts $104\text{--}130\mu$ long; swimmers 22μ long; widely distributed; British Columbia (Waiiles).

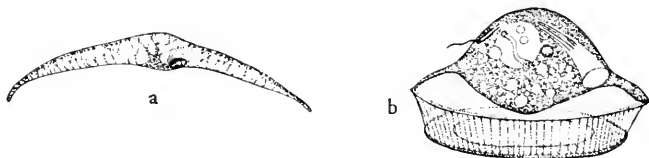


FIG. 106. a, *Leptodiscus medusoides*, $\times 50$ (Hertwig); b, *Craspedotella pileolus*, $\times 110$ (Kofoid).

Suborder 3 Cystoflagellata Haeckel

Since Noctiluca which had for many years been placed in this suborder has been removed, according to Kofoid, to the second suborder, the Cystoflagellata becomes a highly ill-defined group and includes two peculiar marine forms: *Leptodiscus medusoides* Hertwig (Fig. 106, *a*), and *Craspedotella pileolus* Kofoid (Fig. 106, *b*), both of which are medusoid in general body form.

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CHAPTER 12

Subclass 2 **Zoomastigina** Doflein

THE Zoomastigina lack chromatophores and their body organizations vary greatly from a single to a very complex type. The majority possess a single nucleus which is, as a rule, vesicular in structure. A characteristic organella, the parabasal body (p. 66) is present in numerous forms and myonemes are found in some species. Nutrition is holozoic or saprozoic (parasitic). Asexual reproduction is by longitudinal fission; sexual reproduction is unknown. Encystment occurs commonly. The Zoomastigina are free-living or parasitic in various animals.

With pseudopodia besides flagella.....Order 1 Rhizomastigina
With flagella only

With 1-2 flagella.....Order 2 Protomonadina (p. 239)

With 3-8 flagella.....Order 3 Polymastigina (p. 260)

With more than 8 flagella.....Order 4 Hypermastigina (p. 277)

Order 1 **Rhizomastigina** Bütschli

A number of borderline forms between the Sarcodina and the Mastigophora are placed here. Flagella vary in number from one to several and pseudopods also vary greatly in number and in appearance.

With many flagella.....Family 1 Multiciliidae

With 1-3 rarely 4 flagella.....Family 2 Mastigamoebidae (p. 236)

Family 1 **Multiciliidae** Poche

Genus **Multicilia** Cienkowski. Generally spheroidal, but amoeboid; with 40-50 flagella, long and evenly distributed; one or more nuclei; holozoic; food obtained by means of pseudopodia; contractile vacuoles numerous; multiplication by fission; fresh or salt water.

M. marina C. (Fig. 107, *a*). 20-30 μ in diameter; uninucleate; salt water.

M. lacustris Lauterborn (Fig. 107, *b*). Multinucleate; 30-40 μ in diameter; fresh water.

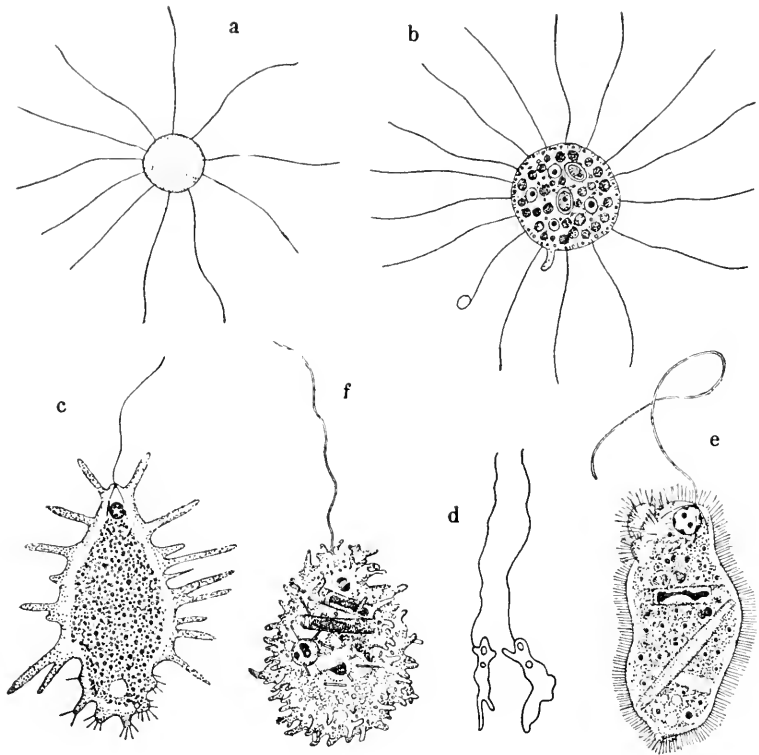


FIG. 107. a, *Multicilia marina*, $\times 400$ (Cienkowski); b, *M. lacustris*, $\times 400$ (Lauterborn); c, *Mastigamoeba aspera*, $\times 200$ (Schulze); d, *M. longifilum*, $\times 340$ (Stokes); e, *M. setosa*, $\times 370$ (Goldschmidt); f, *Mastigella vitrea*, $\times 370$ (Goldschmidt).

Family 2 Mastigamoebidae

With 1–3 or rarely 4 flagella and axopodia or lobopodia; uninucleate; flagellum arises from a basal granule which is often connected with the nucleus by a rhizoplast; binary fission in both trophic and encysted stages; sexual reproduction has been reported in one species; holozoic or saprozoic; the majority are free-living, though a few parasitic.

Genus **Mastigamoeba** Schulze (*Mastigina* Frenzel). Monomastigote, uninucleate, with finger-like pseudopodia; flagellum long and connected with nucleus; fresh water, soil or endocommensal.

M. aspera S. (Fig. 107, c). Subspherical or oval; during locomotion elongate and narrowed anteriorly, while posterior end rounded or lobed; numerous pseudopods slender, straight; nucleus near flagellate end; 2 contractile vacuoles; $150\text{--}200\mu$ by about 50μ ; in ooze of pond.

M. longifilum Stokes (Fig. 107, d). Elongate, transparent flagellum twice body length; pseudopods few, short; contractile vacuole anterior; body 28μ long when extended, contracted about 10μ stagnant water.

M. setosa (Goldschmidt) (Fig. 107, e). Up to 140μ long.

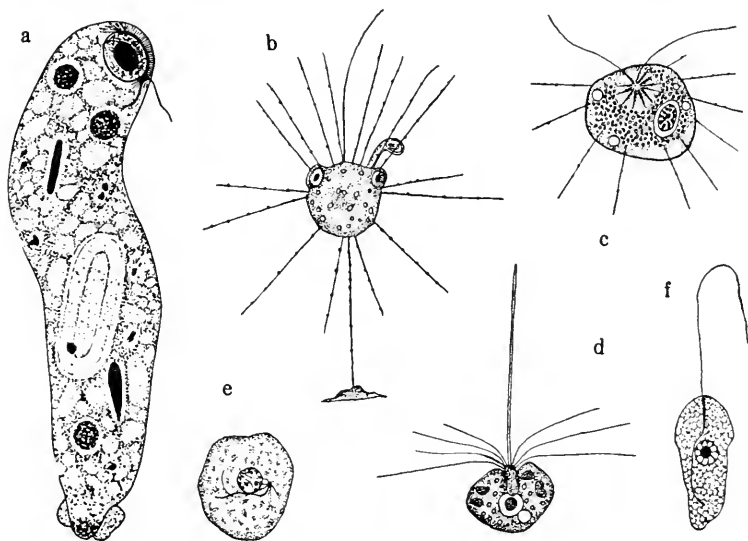


FIG. 108. a, *Mastigamoeba hylae*, $\times 690$ (Becker); b, *Actinomonas mirabilis*, $\times 1140$ (Griessmann); c, *Dimorpha mutans*, $\times 940$ (Blochmann); d, *Pteridomonas pulex*, $\times 540$ (Penard); e, *Histomonas meleagridis*, $\times 940$ (Tyzzer); f, *Rhizomastix gracilis*, $\times 1340$ (Mackinnon).

M. hylae (Frenzel) (Fig. 108, a). In hind gut of frogs and tadpoles; $80\text{--}100\mu$ by 20μ ; flagellum about 10μ long.

Genus **Mastigella** Frenzl. Flagellum apparently not connected with nucleus; pseudopods numerous, digitate; body form changes actively and continuously; contractile vacuole.

M. vitrea Goldschmidt (Fig. 107, f). 150μ long; sexual reproduction (Goldschmidt).

Genus **Actinomonas** Kent. Generally spheroidal, with a single

flagellum and radiating pseudopods; ordinarily attached to foreign object with a cytoplasmic process, but swims freely by withdrawing it; nucleus central; several contractile vacuoles; holozoic.

A. mirabilis K. (Fig. 108, *b*). Numerous simple filopodia; about 10μ in diameter; flagellum 20μ long; fresh water.

Genus **Dimorpha** Gruber. Ovoid or subspherical; with 2 flagella and radiating axopodia, all arising from an eccentric centriole; nucleus eccentric; pseudopods sometimes withdrawn; fresh water.

D. mutans G. (Fig. 108, *c*). $15\text{--}20\mu$ in diameter; flagella about $20\text{--}30\mu$ long.

Genus **Pteridomonas** Penard. Small, heart-shaped; usually attached with a long cytoplasmic process; from opposite pole there arises a single flagellum, around which occurs a ring of extremely fine filopods; nucleus central; a contractile vacuole; holozoic; fresh water.

P. pulex P. (Fig. 108, *d*). $6\text{--}12\mu$ broad.

Genus **Histomonas** Tyzzer. Parasitic in domestic fowls; body amoeboid with a blepharoplast; indication of flagellum (?); without cytostome.

H. meleagridis (Smith) (Fig. 108, *e*). $12\text{--}21\mu$ long; rounded resistant phase up to 11μ by 9μ ; the cause of the "blackhead" disease of young turkeys, chicken, grouse, and quail (Tyzzer) in which the intestinal mucosa as well as liver tissues become infected by this organism.

Genus **Rhizomastix** Alexeieff. Body amoeboid; nucleus central; blepharoplast located between nucleus and posterior end; a long fiber (rhizostyle) runs from it to anterior end and continues into the flagellum; without contractile vacuole; division in spherical cyst.

R. gracilis A. (Fig. 108, *f*). $8\text{--}14\mu$ long; flagellum 20μ long; in intestine of axolotles and tipulid larvae.

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CHAPTER 13

Order 2 **Protomonadina** Blochmann

THE protomonads possess one or two flagella and are composed of a heterogeneous lot of Protozoa, mostly parasitic, whose affinities to one another are very incompletely known. The body is in many cases plastic, having no definite pellicle, and in some cases amoeboid. The method of nutrition is holozoic, or saprozoic (parasitic). Reproduction is, as a rule, by longitudinal fission, although budding or multiple fission has also been known to occur, while sexual reproduction, though reported in some forms, has not been confirmed.

With 1 flagellum

With cytoplasmic collar

Collar enclosed in jelly Family 1 Phalansteriidae

Collar not enclosed in jelly

Without lorica Family 2 Codosigidae

With lorica Family 3 Bicosoecidae (p. 241)

Without cytoplasmic collar

Free-living Family 4 Oikomonadidae (p. 243)

Parasitic Family 5 Trypanosomatidae (p. 244)

With 2 flagella

With undulating membrane Family 6 Cryptobiidae (p. 252)

Without undulating membrane

Flagella equally long Family 7 Amphimonadidae (p. 253)

Flagella unequally long

no trailing flagellum Family 8 Monadidae (p. 255)

one flagellum trailing Family 9 Bodonidae (p. 256)

Family 1 **Phalansteriidae** Kent

Genus **Phalansterium** Cienkowski. Small, ovoid; one flagellum and a narrow collar; numerous individuals are embedded in gelatinous substance which presents a dendritic form, with protruding flagella; fresh water.

P. digitatum Stein (Fig. 109, *a*). Cells about 17 μ long; oval; colony dendritic; fresh water among vegetation.

Family 2 **Codosigidae** Kent

Small flagellates, sometimes with second flagellum which serves for fixation of body; delicate collar surrounds flagellum; ordina-

rily sedentary forms; if temporarily freed, organisms swim with flagellum directed backward; holozoic on bacteria or saprozoic; often colonial; free-living in fresh water.

Genus **Codosiga** Kent (*Codonocladium* Stein; *Astrosiga* Kent). Individuals clustered at end of a simple or branching stalk; fresh water.

C. utriculus Stokes (Fig. 109, b). About 11μ long; attached to freshwater plants.

C. disjuncta (Fromentel) (Fig. 109, c). In stellate clusters; cells about 15μ long; fresh water.

Genus **Monosiga** Kent. Solitary; with or without stalk; occasionally with short pseudopodia; attached to freshwater plants. Several species.

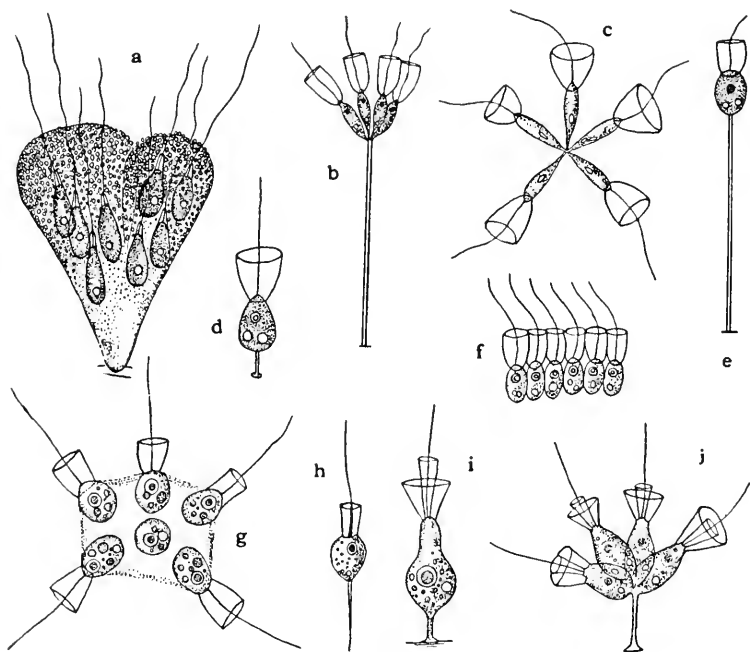


FIG. 109. a, *Phalansterium digitatum*, $\times 540$ (Stein); b, *Codosiga utriculus*, $\times 1340$ (Stokes); c, *C. disjuncta*, $\times 400$ (Kent); d, *Monosiga ovata*, $\times 800$ (Kent); e, *M. robusta*, $\times 770$ (Stokes); f, *Desmarella moniliformis*, $\times 800$ (Kent); g, *Protospongia haeckeli*, $\times 400$ (Lemmermann); h, *Sphaeroeca volvox*, $\times 890$ (Lemmermann); i, *Diplosiga francei*, $\times 400$ (Lemmermann); j, *D. socialis*, $\times 670$ (Francé).

M. ovata K. (Fig. 109, *d*). 5–15 μ long; with a short stalk.

M. robusta Stokes (Fig. 109, *e*). 13 μ long; stalk very long.

Genus **Desmarella** Kent. Cells united laterally to one another; fresh water.

D. moniliformis K. (Fig. 109, *f*). Cells about 6 μ long; cluster composed of 2–12 individuals; standing fresh water.

D. irregularis Stokes. Cluster of individuals irregularly branching, composed of more than 50 cells; cells 7–11 μ long; pond water.

Genus **Protospongia** Kent. Stalkless individuals embedded irregularly in a jelly mass, collars protruding; fresh water.

P. haeckeli K. (Fig. 109, *g*). Body oval; 8 μ long; flagellum 24–32 μ long; 6–60 cells in a colony.

Genus **Sphaeroeca** Lauterborn. Somewhat similar to the last genus; but individuals with stalks and radiating; gelatinous mass spheroidal; fresh water.

S. volvox L. (Fig. 109, *h*). Cells ovoid, 8–12 μ long; stalk about twice as long; flagellum long; contractile vacuole posterior; colony 82–200 μ in diameter; fresh water.

Genus **Diplosiga** Frenzel (*Codonosigopsis* Senn). With 2 collars; without lorica; a contractile vacuole; solitary or clustered (up to 4); fresh water.

D. francei Lemmermann (Fig. 109, *i*). With a short pedicle; 12 μ long; flagellum as long as body.

D. socialis F. (Fig. 109, *j*). Body about 15 μ long; usually 4 clustered at one end of stalk (15 μ long).

Family 3 Bicosoecidae Poche

Small monomastigote; with lorica; solitary or colonial, collar may be rudimentary; holozoic; fresh water.

Genus **Bicosoeca** James-Clark. With vase-like lorica; body small, ovoid with rudimentary collar, a flagellum extending through it; protoplasmic body anchored to base by a cytoplasmic filament (flagellum?); a nucleus and a contractile vacuole; attached or free-swimming.

B. socialis Lauterborn (Fig. 110, *a*). Lorica cylindrical, 23 μ by 12 μ ; body about 10 μ long; often in groups; free-swimming in fresh water.

Genus **Salpingoeca** James-Clark. With a vase-like chitinous lorica to which stalked or stalkless organism is attached; fresh or salt water. Numerous species.

S. fusiformis Kent (Fig. 110, b). Lorica short vase-like, about $15-16\mu$ long; body filling lorica; flagellum as long as body; fresh water.

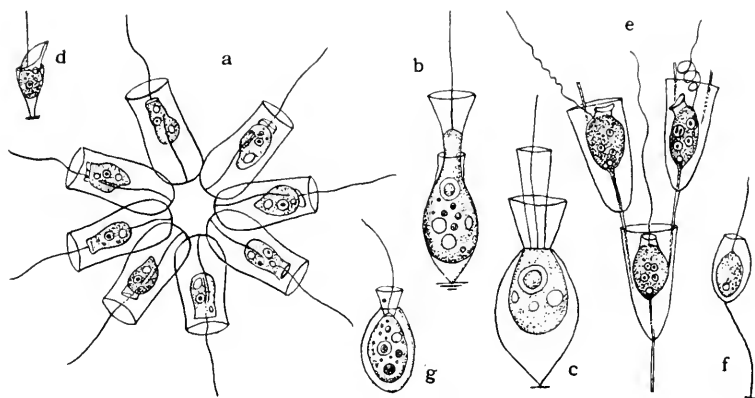


FIG. 110. a, *Bicosoeca socialis*, $\times 560$ (Lauterborn); b, *Salpingoeca fusiformis*, $\times 400$ (Lemmermann); c, *Diplosigopsis affinis*, $\times 590$ (Francé); d, *Histiona zachariasi*, $\times 440$ (Lemmermann); e, *Poteriodendron petiolatum*, $\times 440$ (Stein); f, *Codonoeca inclinata*, $\times 540$ (Kent); g, *Lagenoeca ovata*, $\times 400$ (Lemmermann).

Genus **Diplosigopsis** Francé. Similar to *Diplosiga* (p. 241), but with lorica; solitary; fresh water on algae.

D. affinis Lemmermann (Fig. 110, c). Chitinous lorica, spindle-form, about 15μ long; body not filling lorica; fresh water.

Genus **Histiona** Voigt. With lorica; but body without attaching filament; anterior end with lips and sail-like projection; fresh water.

H. zachariasi V. (Fig. 110, d). Lorica cup-like; without stalk; about 13μ long; oval body 13μ long; flagellum long; standing fresh water.

Genus **Poteriodendron** Stein. Similar to *Bicosoeca*; but colonial; lorica vase-shaped; with a prolonged stalk; fresh water.

P. petiolatum (S.) (Fig. 110, e). Lorica $17-50\mu$ high; body $21-35\mu$ long; flagellum twice as long as body; contractile vacuole terminal; standing fresh water.

Genus **Codonoeca** James-Clark. With a stalked lorica; a single flagellum; 1-2 contractile vacuoles; fresh or salt water.

C. inclinata Kent (Fig. 110, f). Lorica oval; aperture truncate; about 23μ long; stalk twice as long; body oval, about 17μ long;

flagellum 1.5 times as long as body; contractile vacuole posterior; standing fresh water.

Genus **Lagenoecca** Kent. Resembles somewhat *Salpingocca*; with lorica; but without any pedicle between body and lorica; solitary; free-swimming; fresh water.

L. ovata Lemmermann (Fig. 110, *g*). Lorica oval, 15μ long; body loosely filling lorica; flagellum 1.5 times body length; fresh water.

Family 4 Oikomonadidae Hartog

Genus **Oikomonas** Kent. A rounded monomastigote; uninucleate; encystment common; stagnant water, soil and exposed faecal matter.

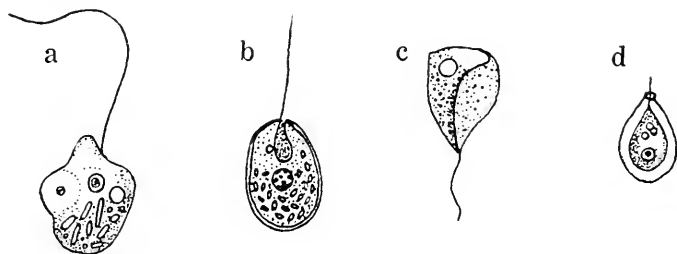


FIG. 111. a, *Oikomonas termo*, $\times 1330$ (Lemmermann); b, *Thylacomonas compressa*, $\times 640$ (Lemmermann); c, *Ancyromonas contorta*, $\times 2000$ (Lemmermann); d, *Platytheca microspora*, $\times 650$ (Stein).

O. termo (Ehrenberg) (Fig. 111, *a*). Spherical or oval; anterior end lip-like; flagellum about twice body length; a contractile vacuole; $5-9\mu$ in diameter; stagnant water.

Genus **Thylacomonas** Schewiakoff. Pellicle distinct; cytostome anterior; one flagellum; contractile vacuole anterior; rare.

T. compressa S. (Fig. 111, *b*). 22μ by 18μ ; flagellum body length; fresh water.

Genus **Ancyromonas** Kent. Ovate to triangular; free-swimming or adherent; flagellum trailing, adhesive or anchorate at its distal end, vibratile throughout remainder of its length; nucleus central; a contractile vacuole; fresh or salt water.

A. contorta (Klebs) (Fig. 111, *c*). Triangular, flattened, posterior end pointed; $6-7\mu$ by $5-6\mu$; flagellum short; a contractile vacuole; standing fresh water.

Genus **Platytheca** Stein. With a flattened pyriform lorica, with a small aperture; 1 or more contractile vacuoles; fresh water.

P. microspora S. (Fig. 111, *d*). Loricæ yellowish brown, with a small aperture; 12–18 μ long; flagellum short; among roots of Lemna.

Family 5 Trypanosomatidae Doflein

Body characteristically leaf-like, although changeable to a certain extent; a single nucleus and a blepharoplast; a flagellum originates in a basal granule which may be independent from, or united with, the blepharoplast (Figs. 9, 112); basal portion of flagellum forms outer margin of undulating membrane which extends along one side of body; exclusively parasitic; a number of important parasitic Protozoa which are responsible for serious diseases of man and domestic animals in various parts of the world are included in it.







In vertebrate host	In invertebrate host				In vertebrate host		
							
Trypanosoma	Trypanosoma	Crithidia	Leptomonas	Leishmania	Leishmania		
			Leptomonas and Phytomonas (in plant)				
			Leishmania				
		Crithidia					
	Herpetomonas						
	Trypanosoma						

FIG. 112. Diagram illustrating the structural differences among the genera of Trypanosomatidae (Wenyon).

Genus **Trypanosoma** Gruby. Parasitic in the circulatory system of vertebrates; highly flattened, pointed at flagellate end, and bluntly rounded, or pointed, at other; polymorphism due to differences in development common; nucleus central; near bluntly rounded end, there is a blepharoplast and usually a basal granule from which the flagellum arises and runs toward opposite end, marking the outer boundary of the undulating membrane; in

most cases flagellum extends freely beyond body; many with myonemes; multiplication by binary or multiple fission. The organism is carried from host to host by blood-sucking invertebrates and undergoes a series of changes in the digestive system of the latter (Fig. 113). A number of forms are pathogenic to their hosts and the diseased condition is termed *trypanosomiasis* in general.

T. gambiense Dutton (Fig. 114, *a*). Parasitic in blood and lymph of man in certain regions of Africa; transmitted by the tsetse fly, *Glossina palpalis*; reservoir hosts are domestic and wild animals. Body 15–30 μ long; mature forms slender and long, with a long flagellum; individuals formed by longitudinal fission short and broad with no projecting flagellum; half-grown forms intermediate in size and structure; the cause of the “sleeping sickness” of man in Africa.

T. (Schizotrypanum) cruzi (Chagas) (Fig. 114, *b*). Parasitic in children in South America (Brazil, Peru, Venezuela, etc.). A small curved form about 20 μ long; nucleus central; blepharoplast large, located close to sharply pointed non-flagellate end; multiplication takes place in the cells of nearly every organ of the host body; upon entering a host cell, the trypanosome loses its flagellum and undulating membrane, and assumes a leishmania form which measures 2 to 5 μ in diameter; this form undergoes repeated binary fission, and a large number of daughter individuals are produced; they develop sooner or later into trypanosomes which, through rupture of host cell, become liberated into blood stream; transmitted by the reduviid bug, *Triatoma megista* and allied species; the diseased condition is known as “Chagas’ disease.” Apparently the organism occurs in wood rats (*Neotoma*) and meadow mice (*Microtus*) in south-western United States, transmitted from host to host by the cone-nose or kissing bug, *Triatoma protracta* (Kofoid and others).

T. brucei Plimmer et Bradford (Figs. 9, *a*; 114 *c*). Polymorphic; 15–30 μ long (average 20 μ); transmitted by various species of tsetse flies, *Glossina*; the most virulent of all trypanosomes; the cause of the fatal disease known as “nagana” among mules, donkeys, horses, camels, cattle, swine, dogs, etc., which terminates in the death of the host animal in from two weeks to a few months; wild animals are equally susceptible; the disease occurs, of course, only in the region in Africa where the tsetse flies live.

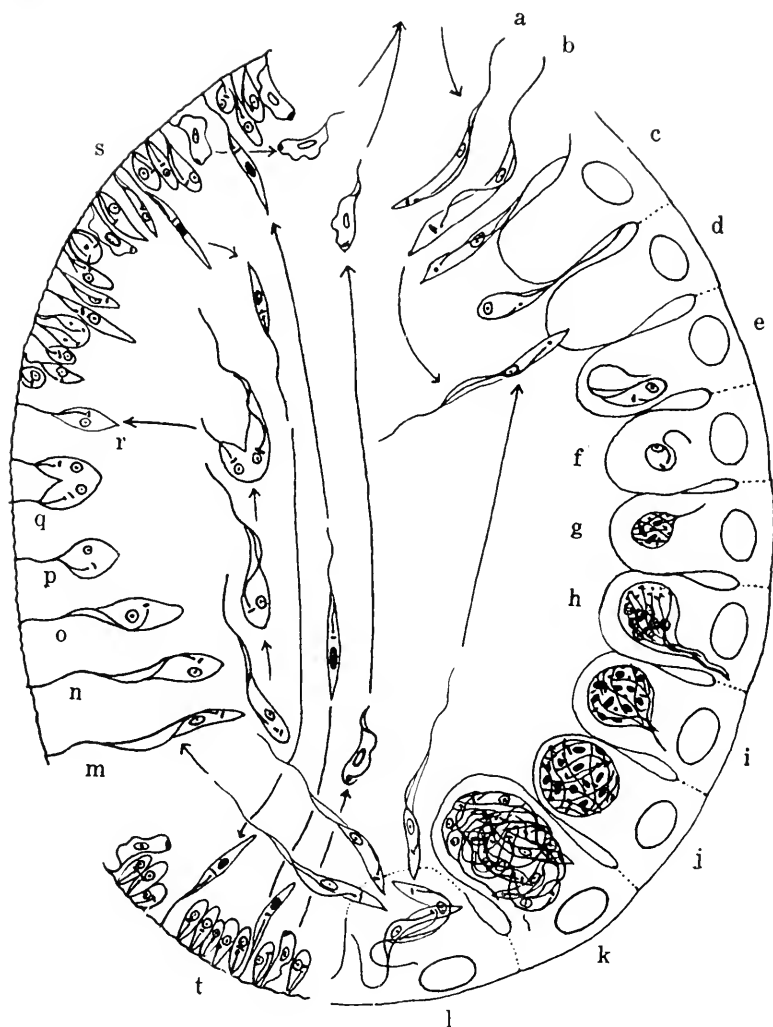


FIG. 113. The life-cycle of *Trypanosoma lewisi* in the flea, *Ceraophyllus fasciatus* (Minchin and Thomson, modified). a, trypanosome from rat's blood; b, individual after being in flea's stomach for a few hours; c-l, stages in intracellular schizogony in stomach epithelium; m-r, two ways in which rectal phase may arise from stomach forms in rectum; s, rectal phase, showing various types; t, secondary infection of pylorus of hind-gut, showing forms similar to those of rectum.

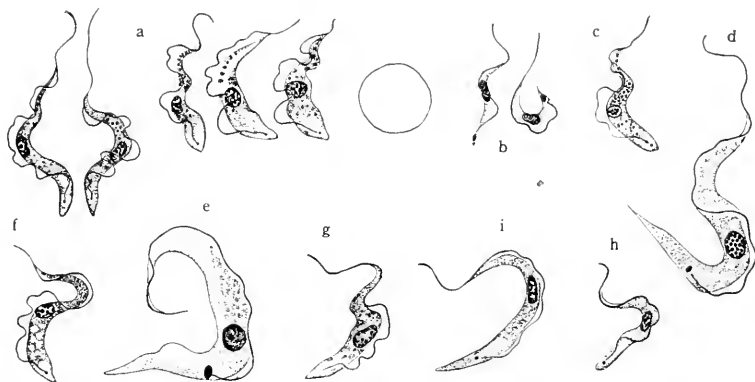


FIG. 114. a, *Trypanosoma gambiense* (5 individuals) and a human erythrocyte; b, *T. cruzi*; c, *T. brucei*; d, *T. theileri*; e, *T. melophagium*; f, *T. evansi*; g, *T. equinum*; h, *T. equiperdum*, all $\times 1000$ (various investigators).

T. theileri Laveran (Fig. 114, d). Non-pathogenic large trypanosome which occurs in blood of cattle; sharply pointed at both ends; $60-70\mu$ long; myonemes are well developed.

T. americanum Crawley. In American cattle; probably identical with *T. theileri*; transmitted from cattle to cattle by tabanid flies.

T. melophagium (Flu) (Fig. 114, e). Non-pathogenic trypanosome of the sheep; $50-60\mu$ long with attenuated ends; transmitted by *Melophagus ovinus*.

T. evansi (Steel) (Fig. 114, f). In horses, mules, donkeys, cattle, dogs, camels, elephants, etc.; infection in horses seems to be usually fatal and known as "surra"; about 25μ long; monomorphic; transmitted by tabanid flies; widely distributed.

T. equinum Vages (Fig. 114, g). In horses in South America, causing an acute disease known as "mal de Caderas"; other domestic animals do not suffer as much as do horses; $20-25\mu$ long; without blepharoplast.

T. equiperdum Doflein (Fig. 114, h). In horses and donkeys; causes "dourine," a chronic disease; widely distributed; $25-30\mu$ long; no intermediate host; transmission takes place directly from host to host during sexual act.

T. lewisi (Kent) (Figs. 113; 114, i). In blood of various species of rat; widely distributed; non-pathogenic under ordinary conditions; about 25μ long; very active; slender; with a long flagellum;

transmitted by the flea, *Ceratophyllus fasciatus*, in which the organism undergoes changes (Fig. 113); when, a rat swallows freshly voided faecal matter containing the organisms, it becomes infected.

T. duttoni Thiroux. In the mouse; similar to *T. lewisi*, but rats are not susceptible, hence considered as a distinct species; transmission by fleas.

T. peromysci Watson. Similar to *T. lewisi*; in Canadian deer mice, *Peromyscus maniculatus* and others.

T. nabiasi Railliet. Similar to *T. lewisi*; in rabbits, *Lepus domesticus* and *L. cuniculus*.

T. paddae Laveran et Mesnil. In Java sparrow, *Munia oryzivora*.

T. noctuae (Schaudinn). In the little owl, *Athene noctua*.

Several other species are known.

Crocodiles, snakes, and turtles are hosts for Trypanosoma. Transmission by blood-sucking arthropods or leeches.

T. rotatorium (Meyer) (Fig. 115, *a*). In tadpoles and adults of various species of frog; between a slender form with a long projecting flagellum measuring about 35μ long and a very broad one without free portion of flagellum, various intermediate forms are to be noted in a single host; blood vessels of internal organs, such as kidneys, contain more individuals than the peripheral vessels; nucleus central, hard to stain; blepharoplast small; undulating membrane highly developed; myonemes prominent; multiplication by longitudinal fission; the leech, *Placobdella marginata*, has been found to be the transmitter in some localities.

T. inopinatum Sargent et Sargent (Fig. 115, *b*). In blood of various frogs; slender; $12\text{--}20\mu$ long; larger forms $30\text{--}35\mu$ long; blepharoplast comparatively large; transmitted by leeches.

Numerous species of Trypanosoma have been reported from the frog, but specific identification is indistinct; it is better and safer to hold that they belong to one of the 2 species mentioned above until their development and transmission become known.

T. diemyctyli Tobey (Fig. 115, *c*). In blood of the newt, *Triturus viridescens*; a comparatively large form; slender; about 50μ by $2\text{--}5\mu$; flagellum $20\text{--}25\mu$ long; with well developed undulating membrane.

Both fresh and salt water fish are hosts to different species of trypanosomes; what effects these parasites exercise upon the host

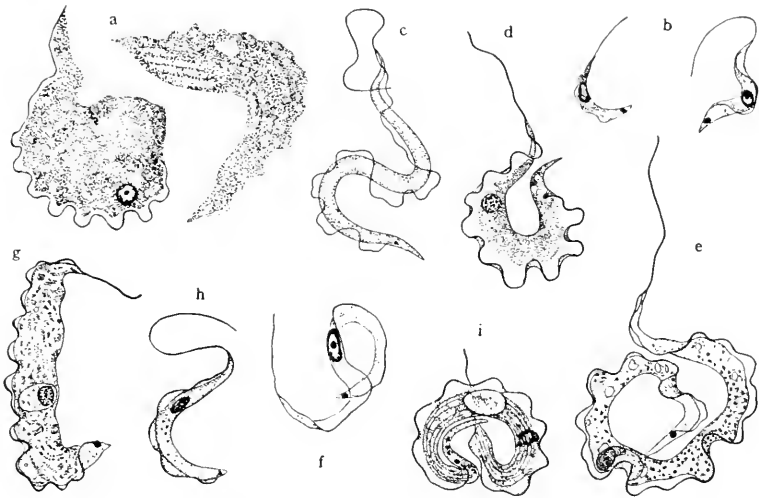


FIG. 115. a, *Trypanosoma rotatorium*, $\times 750$ (Kudo); b, *T. inopinatum*, $\times 1180$ (Kudo); c, *T. diemyctyli*, $\times 800$ (Hegner); d, *T. giganteum*, $\times 500$ (Neumann); e, *T. granulosum*, $\times 1000$ (Minchin); f, *T. remaki*, $\times 1650$ (Kudo); g, *T. percae*, $\times 1000$ (Minchin); h, *T. danilewskyi*, $\times 1000$ (Laveran and Mesnil); i, *T. rajae*, $\times 1600$ (Kudo).

fish are not understood; as a rule, only a few individuals are observed in the peripheral blood of the host.

T. granulosum Laveran et Mesnil (Fig. 115, e). In the eel, *Anguilla vulgaris*; 70–80 μ long.

T. giganteum Neumann (Fig. 115, d). In *Raja oxyrhynchus*; 125–130 μ long.

T. remaki Laveran et Mesnil (Fig. 115, f). In *Esox lucius*, *E. reticulatus* and probably other species; dimorphic; 24–33 μ long.

T. percae Brumpt (Fig. 115, g). In *Perca fluviatilis*; 45–50 μ long.

T. danilewskyi Laveran et Mesnil (Fig. 115, h). In carp and goldfish; widely distributed; 40 μ long.

T. rajae Laveran et Mesnil (Fig. 115, i). In various species of *Raja*; 30–35 μ long.

Genus **Crithidia** Léger. Parasitic in arthropods and other invertebrates; blepharoplast located between central nucleus and flagellum-bearing end (Fig. 112); undulating membrane not so well developed as in *Trypanosoma*; it may lose the flagellum and form a leptomonas or rounded leishmania stage which leaves host

intestine with faecal matter and becomes the source of infection in other host animals.

C. gerridis Patton (Fig. 116, *d*). In intestine of water bugs, *Gerris* and *Microvelia*; 22–45 μ long.

C. hyalommae O'Farrell (Fig. 116, *e, f*). In body cavity of the cattle tick, *Hyalomma aegyptium* in Egypt; the flagellate through its invasion of ova is said to be capable of infecting the offspring while it is still in the body of the parent tick.

C. euryophthalmi McCulloch (Fig. 116, *a-c*). In gut of *Euryophthalmus convivus*; California coast.

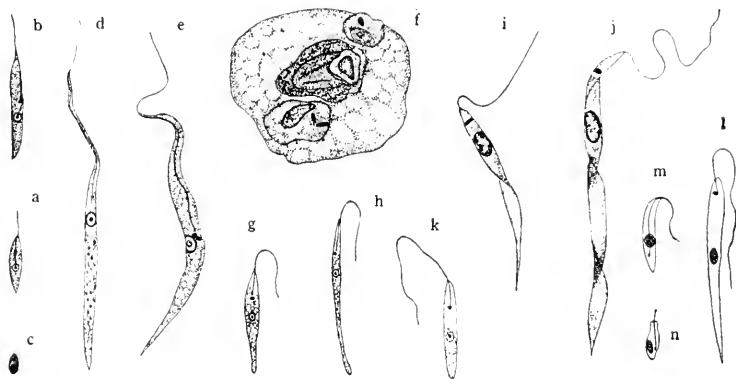


FIG. 116. *a-c*, *Crithidia euryophthalmi* (*a, b*, in mid-gut; *c*, in rectum), $\times 880$ (McCulloch); *d*, *C. gerridis*, $\times 1070$ (Becker); *e, f*, *C. hyalommae*, $\times 1000$ (O'Farrell); *g, h*, *Leptomonas ctenocephali*, $\times 1000$ (Wenyon); *i, j*, *Phytomonas elmassiani* (*i*, in milkweed, *Asclepias* sp.; *j*, in gut of a suspected transmitter, *Oncopeltus fasciatus*), $\times 1500$ (Holmes); *k*, *Herpetomonas muscarum*, $\times 1070$ (Becker); *l-n*, *H. drosophilae*, $\times 1000$ (Chatton and Léger).

Genus **Leptomonas** Kent. Exclusively parasitic in invertebrates; blepharoplast very close to flagellate end; without undulating membrane (Fig. 112); non-flagellate phase resembles *Leishmania*.

L. ctenocephali Fantham (Fig. 116, *g, h*). In hindgut of the dog flea, *Ctenocephalus canis*; widely distributed.

Genus **Phytomonas** Donovan. Morphologically similar to *Leptomonas* (Fig. 112); in the latex of plants belonging to the families: Euphorbiaceae, Asclepiadaceae, Apocynaceae, Sapotaceae and Utricaceae; transmitted by hemipterous insects; often found in enormous numbers in localized areas in host plant; infection

spreads from part to part; infected latex is a clear fluid, owing to the absence of starch grains and other particles, and this results in degeneration of the infected part of the plant. Several species.

P. davidi (Lafront). 15–20 μ by about 1.5 μ ; posterior portion of body often twisted two or three times; multiplication by longitudinal fission; widely distributed; in various species of *Euphorbia*.

P. elmassiani (Migone) (Fig. 116, *i, j*). In various species of milk-weeds; 9–20 μ long; suspected transmitter, *Oncopeltus fasciatus* (Holmes); in South and North America.

Genus **Herpetomonas** Kent. Ill-defined genus (Fig. 112); exclusively invertebrate parasites; Trypanosoma-, Crithidia-, Leptomonas-, and Leishmania-forms occur during development. Several species.

H. muscarum (Leidy) (*H. muscae-domesticae* (Burnett)) (Fig. 116, *k*). In gut of flies, belonging to the genera *Musca*, *Calliphora*, *Sarcophaga*, *Lucilia*, *Phormia*, etc.; up to 30 μ by 2–3 μ .

H. drosophilae (Chatton et Alilaire) (Fig. 116, *l–n*). In intestine of *Drosophila confusa*; large leptomonad forms 21–25 μ long, flagellum body-length; forms attached to rectum 4–5 μ long.

Genus **Leishmania** Ross. Parasitic in vertebrate and invertebrate hosts, the latter not having been actually demonstrated, but suspected; non-flagellate and flagellate forms occur (Fig. 112); very minute; in vertebrate host the organism not flagellated; spherical or ovoid, with a definite pellicle; nucleus eccentric; a blepharoplast; 2–5 μ in diameter; organism enters endothelial cells of blood capillaries and mucosae; spleen becomes highly enlarged; transmitting agent believed to be blood-sucking arthropods; in culture, the organism develops into leptomonad forms; 4 “species” in man, all of which are practically indistinguishable morphologically from one another, and 2 of which are considered as identical.

L. donovani (Laveran et Mesnil) (*L. infantum* Nicolle) (Fig. 117, *a–f*). The organism attacks endothelial cells and macrophage of man, causing the disease known as “kala azar”; it occurs in India, China, west to southern Russia, and regions bordering the Mediterranean Sea.

L. tropica (Wright) (Fig. 117, *g, h*). The organism invades exposed skin and sometimes mucous lining of mouth, pharynx, and nose of man; the disease is known as “Oriental sore”; distribution is similar to the above-mentioned species.

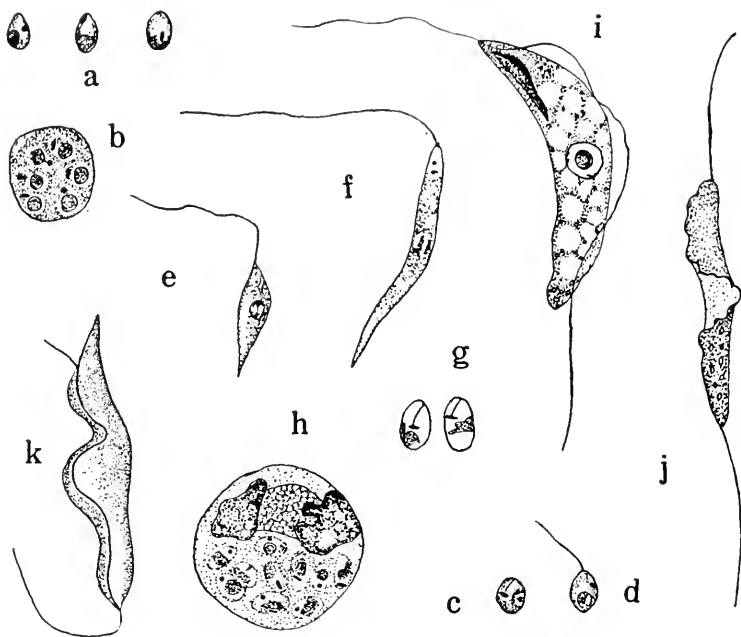


FIG. 117. a-f, *Leishmania donovani* (a, three individuals from lymph smear of a kala azar patient; b, from a spleen smear; c-f, cultural forms), $\times 2000$ (Wenyon; Thomson and Robertson); g, h, *L. tropica* (g, from an Oriental sore; h, the organisms in a polymorphonuclear cell from a sore), $\times 2000$ (Wenyon; Thomson and Robertson); i, *Cryptobia helicis*, $\times 2530$ (Bělař); j, *C. borreli*, $\times 870$ (Mavor); k, *C. cyprini*, $\times 890$ (Plehn).

L. brasiliensis Vianna. The organism occurs in South and Central America; some authors consider this species as identical with *L. tropica*.

Although morphologically identical, these species show specific serum reactions.

Family 6 **Cryptobiidae** Poche

Biflagellate trypanosome-like protomonads; 1 flagellum free, the other marks outer margin of undulating membrane; blepharoplast an elongated rod-like structure, often referred to as the parabasal body; all parasitic.

Genus **Cryptobia** Leidy (*Trypanoplasma* Laveran et Mesnil). Parasitic in reproductive organs of molluscs and other invertebrates and in blood and gut of fish.

C. heliciis L. (Fig. 117, *i*). In reproductive organs of various species of *Helix* in America and Europe; 6–20 μ long; asexual reproduction through binary fission.

C. borreli (Laveran et Mesnil) (Fig. 117, *j*). In blood of various freshwater fish such as *Catostomus*, *Cyprinus*, etc.; 20–25 μ long.

C. cyprini (Plehn) (Fig. 117, *k*). In blood of carp and goldfish; 10–30 μ long; rare.

C. grobbeni (Keysselitz). In coelenteric cavity of Siphonophora; about 65 μ by 4 μ .

Family 7 Amphimonadidae Kent

Body naked or with a gelatinous envelope; 2 equally long anterior flagella; often colonial; 1–2 contractile vacuoles; free-swimming or attached; mainly fresh water.

Genus **Amphimonas** Dujardin. Small oval or rounded amoeboid; flagella at anterior end; free-swimming or attached by an elongated stalk-like posterior process; fresh or salt water.

A. globosa Kent (Fig. 118, *a*). Spherical; about 13 μ in diameter; stalk long, delicate; fresh water.

Genus **Spongomonas** Stein. Individuals in granulated gelatinous masses; flagella with 2 basal granules; one contractile vacuole; colony often several centimeters high; with pointed pseudopodia in motile stage; fresh water.

S. uvella S. (Fig. 118, *b*). Oval; 8–12 μ long; flagella 2–3 times as long; colony about 50 μ high; fresh water.

Genus **Cladomonas** Stein. Individuals are embedded in dichotomous dendritic gelatinous tubes which are united laterally; fresh water.

C. fruticulosa S. (Fig. 118, *c*). Oval; about 8 μ long; colony up to 85 μ high.

Genus **Rhipidodendron** Stein. Similar to *Cladomonas*, but tubes are fused lengthwise; fresh water.

R. splendidum S. (Fig. 118, *d, e*). Oval; about 13 μ long; flagella about 2–3 times body length; fully grown colony 350 μ high.

Genus **Spiromonas** Perty. Elongate; without gelatinous covering; spirally twisted; 2 flagella anterior; solitary; fresh water.

S. augusta (Dujardin) (Fig. 118, *f*). Spindle-form; about 10 μ long; stagnant water.

Genus **Diplomita** Kent. With transparent lorica; body attached to bottom of lorica by a retractile filamentous process; a rudimentary stigma (?); fresh water.

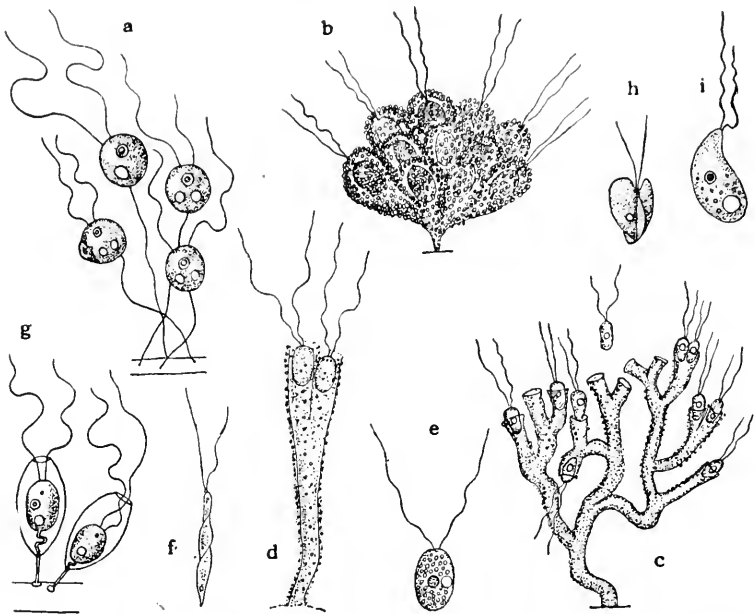


FIG. 118. a, *Amphimonas globosa*, $\times 540$ (Kent); b, *Spongomonas urella*, $\times 440$ (Stein); c, *Cladomonas fruticulosa*, $\times 440$ (Stein); d, e, *Rhipidodendron splendidum* (d, a young colony, $\times 440$; e, a free-swimming individual, $\times 770$) (Stein); f, *Spiromonas augusta*, $\times 1000$ (Kent); g, *Diplomita socialis*, $\times 1000$ (Kent); h, *Streptomonas cordata*, $\times 890$ (Lemmermann); i, *Dinomonas vorax*, $\times 800$ (Kent).

D. socialis K. (Fig. 118, g). Oval; flagellum about 2–3 times the body length; lorica yellowish or pale brown; broadly spindle in form; about 15μ long; pond water.

Genus **Streptomonas** Klebs. Free-swimming; naked; distinctly keeled; fresh water.

S. cordata (Perty) (Fig. 118, h). Heart-shaped; 15μ by 13μ ; rotation movement.

Genus **Dinomonas** Kent. Ovate or pyriform, plastic, free-swimming; 2 flagella, equal or sub-equal, inserted at anterior extremity, where large oral aperture visible only at time of food ingestion, is also located, feeding on other flagellates; vegetative infusions.

D. vorax K. (Fig. 118, i). Ovoid, anterior end pointed; $15\text{--}16\mu$ long; flagella longer than body; hay infusion and stagnant water.

Family 8 **Monadidae** Stein

2 unequal flagella; one primary and the other secondary; motile or attached; 1–2 contractile vacuoles; colony formation frequent; free-living.

Genus **Monas** Müller (*Physomonas* Kent). Plastic and actively motile (“dancing movement”); often attached to foreign objects; not longer than 20μ ; known for a long time, but still very incompletely. Krijgsman (1925) studied the flagellar movements (p. 107).

M. guttula Ehrenberg (Fig. 119, a). Spherical to ovoid; $14\text{--}16\mu$ long; free-swimming or attached; longer flagellum about 1–2 times body length; cysts 12μ in diameter; stagnant water.

M. elongata (Stokes) (Fig. 119, b). Elongate; about 11μ long;

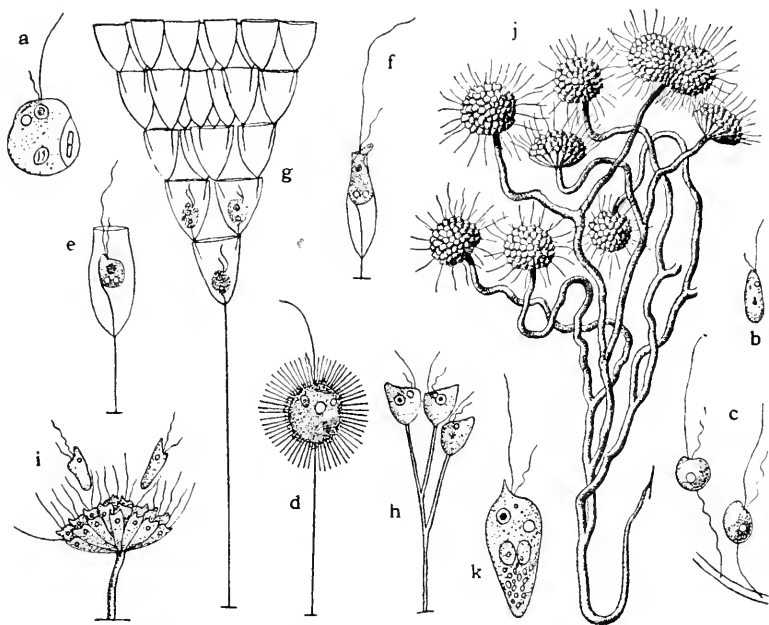


FIG. 119. a, *Monas guttula*, $\times 620$ (Fisch); b, *M. elongata*, $\times 670$ (Stokes); c, *M. socialis*, $\times 670$ (Kent); d, *M. vestita*, $\times 570$ (Stokes); e, *Stokesiclla dissimilis*, $\times 500$ (Stokes); f, *S. leptostoma*, $\times 840$ (Stokes); g, *Stylobryon abbotti*, $\times 480$ (Stokes); h, *Dendromonas virgaria*, a young colony of, $\times 670$ (Stein); i, *Cephalothamnium cyclopum*, $\times 440$ (Stein); j, k, *Anthophysa vegetans* (j, part of a colony, $\times 230$; k, an individual, $\times 770$) (Stein).

free-swimming or attached; anterior end obliquely truncate; fresh water.

M. socialis (Kent) (Figs. 8, *g*; 119, *c*). Spherical; 5–10 μ long; among decaying vegetation in fresh water.

M. vestita (Stokes) (Fig. 119, *d*). Spherical; about 13.5 μ in diameter; stalk about 40 μ long; pond water. Reynolds (1934) made a careful study of the organism.

Genus **Stokesiella** Lemmermann. Body attached by a fine cytoplasmic thread to a delicate and stalked vase-like lorica; 2 contractile vacuoles; fresh water.

S. dissimilis (Stokes) (Fig. 119, *e*). Solitary; lorica about 28 μ long.

S. leptostoma (S.) (Fig. 119, *f*). Lorica about 17 μ long; often in groups; on vegetation.

Genus **Stylobryon** Fromentel. Similar to *Stokesiella*; but colonial; on algae in fresh water.

S. abbotti Stokes (Fig. 119, *g*). Lorica campanulate; about 17 μ long; main stalk about 100 μ high; body oval or spheroidal; flagella short.

Genus **Dendromonas** Stein. Colonial; individuals without lorica, located at end of branched stalks; fresh water among vegetation.

D. virgaria (Weisse) (Fig. 119, *h*). About 8 μ long; colony 200 μ high; pond water.

Genus **Cephalothamnium** Stein. Colonial; without lorica, but individuals clustered at end of a stalk which is colorless and rigid; fresh water.

C. cyclopum S. (Fig. 119, *i*). Ovoid; 5–10 μ long; attached to body of Cyclops and also among plankton.

Genus **Anthophysa** Bory. Colonial forms, somewhat similar to *Cephalothamnium*; stalks yellow or brownish and usually bent; detached individuals amoeboid with pointed pseudopodia.

A. vegetans (Müller) (Fig. 119, *j, k*). About 5–6 μ long; common in stagnant water and infusion.

Family 9 **Bodonidae** Bütschli

With 2 flagella; one directed anteriorly and the other posteriorly and trailing; flagella arise from anterior end which is drawn out to a varying degree; one to several contractile vacuoles; asexual reproduction by binary fission; holozoic or saprozoic (parasitic).

Genus **Bodo** Ehrenberg (*Prowazekia* Hartmann et Chagas). Small, ovoid, but plastic; cytostome anterior; nucleus central or anterior; flagella connected with 2 blepharoplasts in some species; encystment common; in stagnant water and coprozoic. Numerous species.

B. caudatus (Dujardin) (Fig. 120, *a*, *b*). Highly flattened, usually tapering posteriorly; $11-22\mu$ by $5-10\mu$; anterior flagellum about body length, trailing flagellum longer; blepharoplast; cysts spherical; stagnant water.

B. edax Klebs (Fig. 120, *c*). Oval with pointed anterior end; $11-15\mu$ by $5-7\mu$; stagnant water.

Genus **Pleuromonas** Perty. Naked, somewhat amoeboid; usually attached with trailing flagellum; active cytoplasmic movement; fresh water.

P. jaculans P. (Fig. 120, *d*). Body $6-10\mu$ by about 5μ ; flagellum 2-3 times body length; 4-8 young individuals are said to emerge from a spherical cyst; stagnant water.

Genus **Rhynchomonas** Klebs (*Cruzella* Faria, da Cunha et Pinto). Similar to *Bodo*, but there is an anterior extension of body, in which one of the flagella is embedded, while the other flagellum trails; a single nucleus; minute forms; fresh or salt water; also sometimes coprozoic.

R. nasuta (Stokes) (Fig. 120, *e*). Oval, flattened; $5-6\mu$ by $2-3\mu$; fresh water and coprozoic.

R. marina (F., C. et P.). In salt water.

Genus **Proteromonas** Kunstler (*Prowazekella* Alexeieff). Elongated pyriform; 2 flagella from anterior end, one directed anteriorly and the other, posteriorly; nucleus anterior; encysted stage is remarkable in that it is capable of increasing in size to a marked degree; exclusively parasitic; in gut of various species of lizards.

P. lacertae (Grassi) (Figs. 9, *b*; 120, *f*). Elongate, pyriform; $10-30\mu$ long; gut of lizards belonging to the genera *Lacerta*, *Tarentola*, etc.

Genus **Retortamonas** Grassi (*Embadomonas* Mackinnon). Spindle-form or pyriform, drawn out posteriorly; ventral side usually more convex than dorsal side; large oval pouch on ventral side, about $1/3$ as long as body; nucleus anterior; 2 flagella longer than body, anterior flagellum shorter than the posterior one which usually shows 2 or 3 undulations; cysts ovoid; parasitic in gut of various animals.

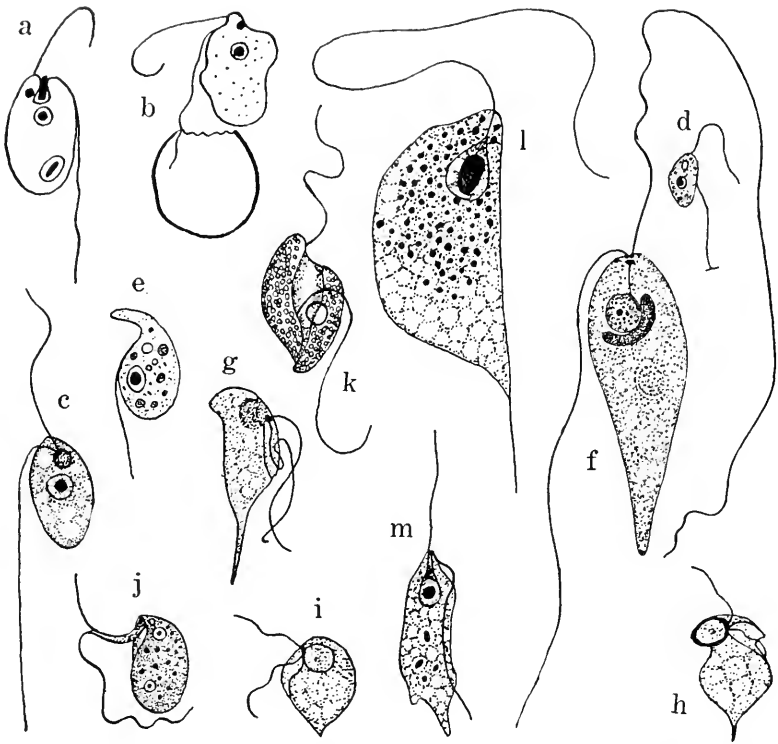


FIG. 120. a, b, *Bodo caudatus*, $\times 1500$ (Sinton); c, *B. edax*, $\times 1400$ (Kühn); d, *Pleuromonas jaculans*, $\times 650$ (Lemmermann); e, *Rhinchomonas nasuta*, $\times 1800$ (Parisi); f, *Proteromonas lacertae*, $\times 2500$ (Kühn); g, *Retortamonas gryllotalpae*, $\times 2000$ (Wenrich); h, *R. blattae*, $\times 2000$ (Wenrich); i, *R. intestinalis*, $\times 2000$ (Wenrich); j, *Phyllomitus undulans*, $\times 1000$ (Stein); k, *Colponema loxodes*, $\times 650$ (Stein); l, *Cercomonas longicauda*, $\times 2000$ (Wenyon); m, *C. crassicauda*, $\times 2000$ (Dobell).

R. gryllotalpae (G.) (Fig. 120, g). About $7-14\mu$ (average 10μ) long; in intestine of the mole cricket, *Gryllotalpa gryllotalpa*.

R. blattae (Bishop) (Fig. 120, h). About $6-9\mu$ long; in colon of cockroaches.

R. intestinalis (Wenyon et O'Connor) (Fig. 120, i). $6-14\mu$ long; in human intestine.

Genus **Phyllomitus** Stein. Oval; highly plastic; cytostome large and conspicuous; 2 unequal flagella, each originates in a basal granule; apparently no blepharoplast; fresh water or coprozoic.

P. undulans S. (Fig. 120, *j*). Ovoid; 21–27 μ long; trailing flagellum much longer than anterior one; stagnant water.

Genus **Colponema** Stein. Body small; rigid; ventral furrow conspicuous, wide at anterior end; one flagellum arises from anterior end and the other from middle of body; fresh water.

C. loxodes S. (Fig. 120, *k*). 18–30 μ by 14 μ ; cytoplasm with refractile globules.

Genus **Cercomonas** Dujardin. Biflagellate, both flagella arising from anterior end of body; one directed anteriorly and the other runs backward over body surface, becoming a trailing flagellum; plastic; pyriform nucleus connected with the basal granules of flagella; spherical cysts uninucleate; fresh water or coprozoic.

C. longicauda D. (Fig. 120, *l*). Pyriform or ovoid; posterior end drawn out; 18–36 μ by 9–14 μ ; flagella as long as body; pseudopodia; fresh water and coprozoic.

C. crassicauda D. (Fig. 120, *m*). 10–16 μ by 7–10 μ ; fresh water and coprozoic.

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CHAPTER 14

Order 3 **Polymastigina** Blochmann

THE Zoomastigina placed in this group possess 3–8 (in one family up to a dozen or more) flagella and generally speaking, are minute forms with varied characters and structures. Many possess a cytosome and one to many nuclei and the body is covered by a thin pellicle which allows the organism to change form, although each species shows a typical form. The cytoplasm does not show any special cortical differentiation; in many, there is an axial structure known as axostyle or axostylar filaments (p. 61). In forms with an undulating membrane, there is usually a rod-like structure beneath the membrane which is known as costa (Kunstler). Parabasal body of various forms occur in many species. The majority of Polymastigina inhabit the digestive tract of animals and nutrition is holozoic or saprozoic (parasitic). Asexual reproduction is by longitudinal fission, sometimes multiple. Encystment is common, and the cyst is responsible for infection of new hosts through mouth. Sexual reproduction has not been definitely established.

- With 1 nucleus.....Suborder 1 Monomonadina
- With 2 nuclei.....Suborder 2 Diplomonadina (p. 272)
- With more than 2 nuclei.....Suborder 3 Polymonadina (p. 274)

Suborder 1 **Monomonadina**

- Without axial organella
 - With 3 flagella.....Family 1 Trimastigidae
 - With 4 flagella
 - None undulates on body surface...*.....
 -Family 2 Tetramitidae (p. 263)
 - One undulates on body surface.....
 -Family 3 Chilomastigidae (p. 264)
 - With more than 4 flagella.....Family 4 Callimastigidae (p. 265)
- With axial organella
 - Without undulating membrane..Family 5 Polymastigidae (p. 265)
 - With undulating membrane..Family 6 Trichomonadidae (p. 269)

Family 1 **Trimastigidae** Kent

Free-swimming or attached; with 3 flagella; no cytostome; free-living in fresh or salt water, coprozoic or parasitic.

Genus **Trimastix** Kent. Ovate or pyriform; naked; free-swimming; with a laterally produced membranous border; 3 flagella, 1 anterior flagellum vibrating, 2 trailing; salt water.

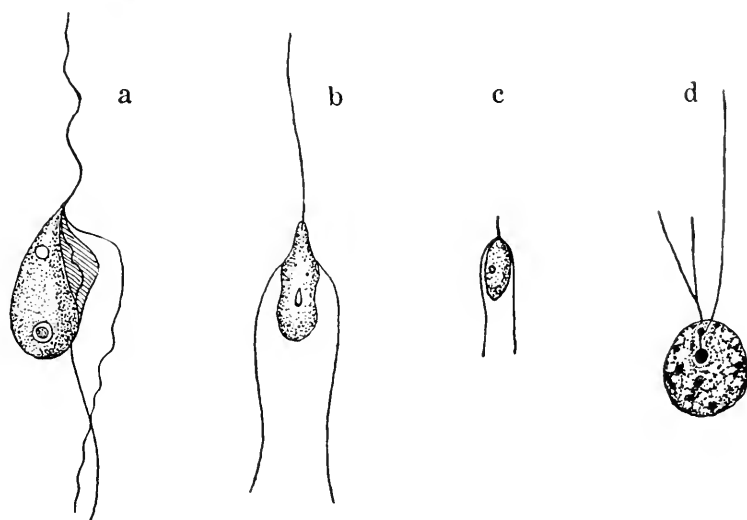


FIG. 121. a, *Trimastix marina*, $\times 1250$ (Kent); b, *Dallingeria drysdali*, $\times 2000$ (Kent); c, *Macromastix lapsa*, $\times 1500$ (Stokes); d, *Enteromonas hominis*, $\times 2000$ (da Fonseca).

T. marina K. (Fig. 121, a). About 18μ long; salt water.

Genus **Dallingeria** Kent. Free-swimming or attached; with trailing flagella; body small; with drawn-out anterior end; fresh water with decomposed organic matter.

D. drysdali K. (Fig. 121, b). Small; elongate oval; less than 6μ long; stagnant water.

Genus **Macromastix** Stokes. Free-swimming, somewhat like *Dallingeria*, but anterior region not constricted; 3 flagella from anterior end; one contractile vacuole; fresh water.

M. lapsa S. (Fig. 121, c). Ovoid; 5.5μ long; anterior flagellum $1/2$ and trailing flagella 2–3 times body length; pond water.

Genus **Enteromonas** da Fonseca. Body globular; 2 anterior flagella and one trailing flagellum.

E. hominis d. F. (Fig. 121, d). Small, $5\text{--}6\mu$ in diameter; in human faeces.

Genus **Mixotricha** Sutherland. Large; elongate; anterior tip spirally twisted and motile; posterior end probably eversible;

body surface with a coat of cilia in closely packed transverse bands (insertion and movement entirely different from those of *Trichonympha*) except posterior end; 3 short flagella at anterior end; nucleus, 20μ by 2μ , connected with blepharoplasts by pro-

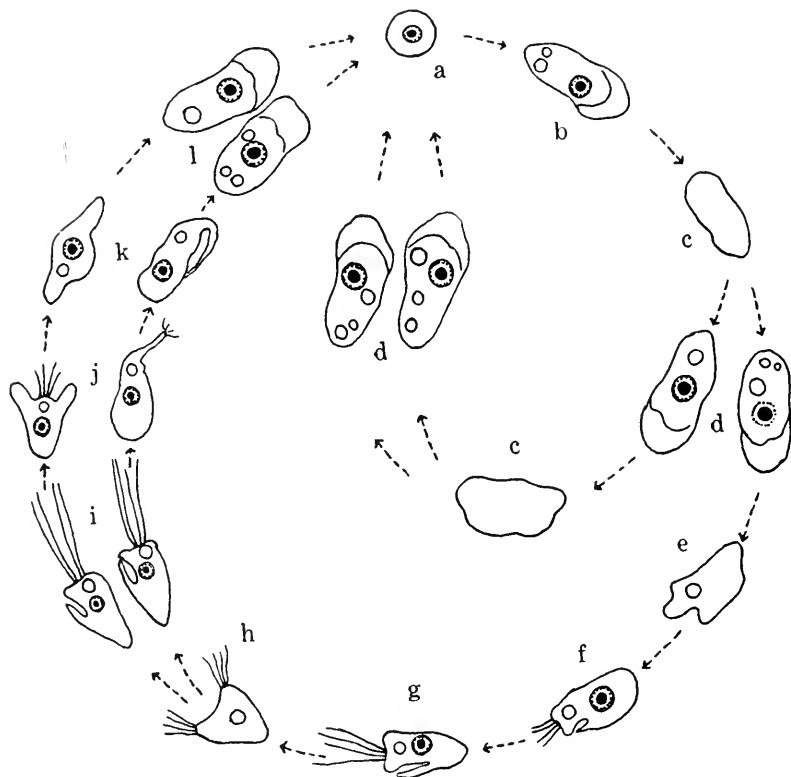


FIG. 122. Diagram illustrating the life-cycle of *Tetramitus rostratus* (Bunting). a, cyst; b, vegetative amoeba; c, division; d, after division; e, f, stages in transformation to flagellate form; g, fully formed flagellate; h, flagellate prior to division; i, flagellate after division; j-l, transformation stages to amoeba.

longed tube which encloses nucleus itself; cytoplasm with scattered wood chips; in termite gut. One species. Taxonomic position undetermined.

M. paradoxa S. About 340μ long, 200μ broad and 25μ thick; in gut of *Mastotermes darwiniensis*; Australia.

Family 2 Tetramitidae Bütschli

With 4 flagella, no one of which undulates on body surface.

Genus **Tetramitus** Perty. Ellipsoidal or pyriform; free-swimming; cytostome at anterior end; 4 flagella unequal in length; a contractile vacuole; holozoic; fresh or salt water.

T. rostratus P. (Fig. 123, a). Form variable; usually ovoid with narrow posterior region; 18–30 μ by 8–11 μ ; stagnant water. Bunting (1922, 1926) observed a very interesting life-cycle of an organism which she found in culture of caecal contents of rat and which she identified as *T. rostratus* (Fig. 122).

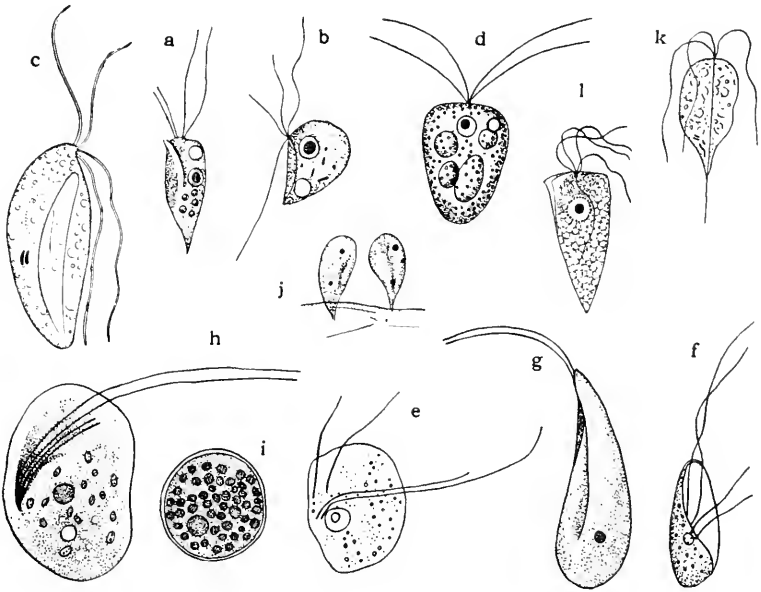


FIG. 123. a, *Tetramitus rostratus*, $\times 620$ (Lemmermann); b, *T. pyriformis*, $\times 670$ (Klebs); c, *T. salinus*, $\times 1630$ (Kirby); d, *Collodictyon triciliatum*, $\times 400$ (Carter); e–j, *Costia necatrix* (e, f, $\times 800$ (Weltner); g–i, $\times 1400$ (Moroff); j, two individuals attached to host integument $\times 500$ (Kudo)); k, *Tricercomonas intestinalis*, $\times 1730$ (Wenyon and O'Connor); l, *Copromastix prowazeki*, $\times 1070$ (Aragão).

T. pyriformis Klebs (Fig. 123, b). Pyriform, with pointed posterior end; 11–13 μ by 10–12 μ ; stagnant water.

T. salinus (Entz) (Fig. 123, c). 2 anterior flagella, 2 long trailing flagella; nucleus anterior; cytostome anterior to nucleus; a

groove to posterior end; cytopharynx temporary and length variable; 20–30 μ long (Entz); 15–19 μ long (Kirby). Kirby observed it in a pool with salinity of about 15 per cent at Marina, California.

Genus **Collodictyon** Carter. Body highly plastic; with longitudinal furrows; posterior end bluntly narrowed or lobed; no apparent cytostome; 4 flagella; a contractile vacuole anterior; fresh water.

C. triciliatum C. (Fig. 123, *d*). Spherical, ovoid or heart-shaped; 27–60 μ long; flagella as long as the body; pond water. Rhodes (1919) made a comprehensive cytological study of the organism.

Genus **Costia** Leclercq. Ovoid in front view; pyriform in profile; toward right side, a funnel-like depression, at the posterior end of which are located cytostome (?) and 2 long and 2 short flagella; contractile vacuole in posterior half; longitudinal division; encystment; ectoparasitic in various freshwater fishes.

C. necatrix (Henneguy) (Fig. 123, *e-j*). 10–20 μ by 5–10 μ ; compact nucleus central; a contractile vacuole; cyst uninucleate, spherical, 7–10 μ in diameter; when present in large numbers, the epidermis of fish appears to be covered by a whitish coat.

Genus **Tricercomonas** Wenyon et O'Connor. Body similar to that of *Cercomonas* (p. 259), but with 3 anterior flagella and a posterior flagellum; oblong cyst with 4 nuclei when mature; parasitic.

T. intestinalis W. et O'C. (Fig. 123, *k*). 4–8 μ long; in human intestine.

Genus **Copromastix** Aragão. 4 anterior flagella equally long; body triangular or pyramidal; coprozoic.

C. prowazeki A. (Fig. 123, *l*). About 16–18 μ long; in human and rat faeces.

Family 3 **Chilomastigidae** Wenyon

4 flagella, one of which undulates on body surface.

Genus **Chilomastix** Alexeieff. Pyriform; with a large cytostomal cleft at anterior end; nucleus anterior; 3 anteriorly directed flagella; short fourth flagellum undulates within cleft; cysts common; in intestine of vertebrates. Several species.

C. mesnili (Wenyon) (Fig. 124, *a-c*). 10–15 μ long; cyst 5–10 μ long; in human intestine; commensal, although often found in diarrhoeic stools.

C. intestinalis Kuczynski. In guinea pigs.

C. bettencourti da Fonseca. In rats and mice.

C. cuniculi da Fonseca. In rabbits.

C. caprac da Fonseca. In goat.

C. gallinarum Martin et Robertson. 11–20 μ by 5–6 μ ; in domestic fowls.

Family 4 **Callimastigidae** da Fonseca

Flagella 12 or more; in stomach of ruminants or in caecum and colon of horse.

Genus **Callimastix** Weissenberg. Ovoid; compact nucleus central or anterior; 12–15 long flagella near anterior end, vibrate in unison. Weissenberg (1912) considered this genus to be related to *Lophomonas* (p. 280), but organism lacks axial organellae; in *Cyclops* and alimentary canal of ruminants and horse.

C. cyclopis W. In body-cavity of *Cyclops* sp.

C. frontalis Braune (Fig. 124, *d*). 12 flagella; about 12 μ long; flagella 30 μ long; in cattle, sheep and goats.

C. equi Hsiung (Fig. 124, *e*). 12–15 flagella; 12–18 μ by 7–10 μ ; nucleus central; in caecum and colon of horse.

Family 5 **Polymastigidae** Bütschli

With axial structures; without undulating membrane; flagella variable in number.

Genus **Polymastix** Bütschli. Pyriform; 4 flagella arise from 2 blepharoplasts located at anterior end; cytostome and axostyle inconspicuously present; ectoplasm covered by longitudinal ridges; endocommensal in insects.

P. melolonthae (Grassi) (Fig. 124, *f*). 5–22 μ long; in hindgut of *Melolontha*, *Oryctes*, *Cetonia*, *Rhizotrogus*, *Tipula*, etc.

Genus **Eutrichomastix** Kofoid et Swezy (*Trichomastix* Blochmann). Pyriform; anterior end rounded; cytostome and nucleus anterior; 3 flagella of equal length arise from anterior end, the fourth trailing; axostyle projects beyond posterior end of body; all endocommensal.

E. serpentis (Dobell) (Fig. 124, *g*). About 10–25 μ long; in intestine of snakes; *Pituophis*, *Eutaenia*, and *Python*.

E. batrachorum (Dobell) (Fig. 124, *h*). Ovoid; 6–20 μ long; in intestine of *Rana fusca*.

E. axostylis Kirby (Fig. 124, *i*). Elongate, ellipsoid, or pyriform; axostyle projecting; 5–10.5 μ by 2–3.5 μ ; 3 anterior flagella 5–10 μ long; in gut of *Nasutitermes kirbyi*.

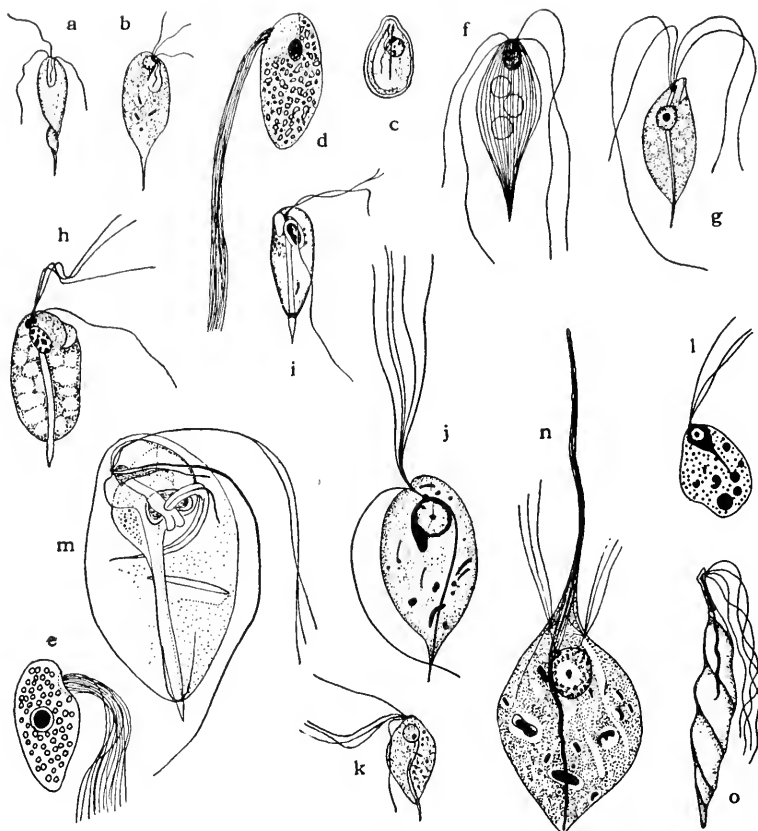


FIG. 124. a-c, *Chilomastix mesnili*, $\times 1350$ (Kudo); d, *Callimastix frontalis*, $\times 1500$ (Braune); e, *C. equi*, $\times 1100$ (Hsiung); f, *Polymastix melolonthae*, $\times 540$ (Hamburger); g, *Eutrichomastix serpentis*, $\times 1450$ (Kofoid and Swezy); h, *E. batrachorum*, $\times 1350$ (Dobell); i, *E. axostylis*, $\times 2000$ (Kirby); j, *Hexamastix termopsidis*, $\times 2670$ (Kirby); k, *H. batrachorum*, $\times 1000$ (Alexeieff); l, *Protrichomonas legeri*, $\times 1000$ (Alexeieff); m, *Parajoenia grassii*, $\times 890$ (Kirby); n, *Oxymonas projector*, $\times 1260$ (Kofoid and Swezy); o, *Streblomastix strix*, $\times 1030$ (Kidder).

Genus **Hexamastix** Alexeieff. Body similar to *Eutrichomastix*, but with 6 flagella, of which one trails; axostyle conspicuous; parabasal body prominent.

H. termopsidis Kirby (Fig. 124, j). Ovoidal or pyriform; 5–11 μ long; flagella 15–25 μ long; in gut of *Zootermopsis angusticollis* and *Z. nevadensis*; California.

H. batrachorum Alexeieff (Fig. 124, *k*). Oval or spindle form; 8–14 μ by 4–8 μ ; flagella about body length; in gut of *Triton taeniatus*.

Genus **Protrichomonas** Alexeieff. 3 anterior flagella of equal length, arising from a blepharoplast located at anterior end; parasitic.

P. legeri A. (Fig. 124, *l*). In oesophagus of the marine fish, *Box boops*.

Genus **Parajoenia** Janicki. Medium large; ends rounded; 3 anterior flagella; 1 long trailing flagellum; axostyle stout; parabasal body in 2 parts; Kirby (1937) showed that this genus belongs to Polymastigina; in termite gut.

P. grassii J. (Fig. 124, *m*). 29–59 μ by 12–33 μ ; numerous spirochaetes, about 15–20 μ long, adherent to anterior and posterior parts of body; in *Neotermes connexus*; Hawaii.

Genus **Oxymonas** Janicki. Oval or pyriform; extensible and retractile rostellum (proboscis) at anterior end; at its base 2 groups of 3 flagella; nucleus anterior; bundle of axial filaments; in termite gut.

O. projector Kofoid et Swezy (Fig. 124, *n*). 12–40 μ long; in *Kaloterms perparvus*.

O. dimorpha Connell. Subovoid; delicate pellicle; axostyle protruding; a pair of long anterior flagella from 2 blepharoplasts connected by rhizoplast; nucleus anterior, Feulgen negative; when attached to intestine, rostellum elongate, flagella disappear; xylophilous; 165–195 μ by 14–17 μ ; in *Neotermes simplicicornis*; California and Arizona.

Genus **Streblomastix** Kofoid et Swezy. Elongate, spindle; 4 anterior flagella; nucleus elongate spindle; with spiral ridges; in termite gut.

S. strix K. et S. (Fig. 124, *o*). 200–530 μ by 20–80 μ ; in *Zootermopsis angusticollis*.

Genus **Devescovina** Foà. Oblong; axostyle rigid, extends to posterior end; 3 anterior flagella and one long trailing flagellum; parabasal body; in termite gut.

D. lemniscata Kirby (Fig. 125, *a*). 12–41 μ by 7–15 μ ; in *Cryptotermes hermsi*.

Genus **Pseudodevescovina** Sutherland. Relatively large and stout; a single anterior flagellum; without (Sutherland) or with one comparatively short trailing flagellum (Kirby); axostyle

stout; parabasal body large; investment of short spirochaetes; in termite gut.

P. uniflagellata S. About 65μ by $40-45\mu$ (Sutherland); $52-95\mu$ by $26-60\mu$ (Kirby); in *Kaloterms insularis*.

Genus **Monocercomonas** Grassi. Small; 4 flagella inserted in pairs in 2 places; 2 directed anteriorly and the other 2, posteriorly; axostyle filamentous; parasitic.

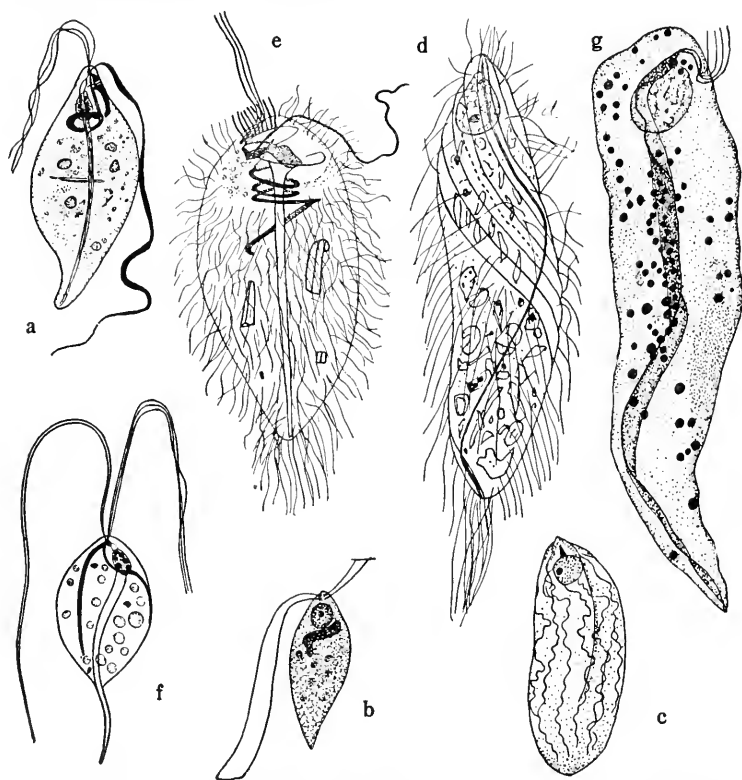


FIG. 125. a, *Devescorina lemniscata*, $\times 1000$ (Kirby); b, *Monocercomonas bufonis*, $\times 1670$ (Alexeieff); c, *Pyrsonympha vertens*, $\times 260$ (Comes); d, *Dinonympha fimbriata*, $\times 830$ (Kirby); e, *Metadevescorina debilis*, $\times 1130$ (Light); f, *Foaina nana*, $\times 1670$ (Kirby); g, *Saccinobaculus ambloaxostylus*, $\times 800$ (Cleveland et al.).

M. bufonis Dobell (Fig. 125, b). Spindle-form; $12-15\mu$ long; cysts spherical; in Axolote, Triton, frogs and toads.

Genus **Pyrsonympha** Leidy. Ovoid or ellipsoid; axostyle divided into 2 parts along its posterior portion and the whole

vibrates in life; 4–8 flagella adhering to the body; in termite gut.

P. vertens L. (Fig. 125, *c*). 100–160 μ long; in *Reticulitermes flavipes*.

Genus **Dinenympha** Leidy. Elongate; 4–8 flagella spirally adhering to the body; axostyle conspicuous; in termite gut.

D. gracilis L. In *Reticulitermes flavipes* and *R. lucifugus*; Duboseq and Grassé hold that this is an immature stage of *Pyrsonympha vertens*.

D. fimbriata Kirby (Fig. 125, *d*). 52–78 μ by about 18 μ ; in *Reticulitermes hesperus*.

Genus **Metadevescovina** Light. Spindle to elongate oval; circular in cross-section; body surface smooth, but often with attached bacteria; nucleus anterior; axostyle not extending beyond the posterior end of body; parabasal body a spiral rod around axostyle; one primary flagellum and 3 long secondary flagella; spirochaetes adhering to body surface (Kirby); in termite gut.

M. debilis L. (Figs. 23; 125, *e*). 30–70 μ by 15–30 μ ; in *Kaloterms hubbardi*.

Genus **Foaina** Janieki (*Paradevescovina* Kirby). Ellipsoidal; rigid axostyle protrudes a little; flagella similar to those of *Devescovina* in number and appearance; parabasal body a long curved rod; in termite gut.

F. nana Kirby (Fig. 125, *f*). 10 μ by 7 μ ; in *Cryptotermes hermsi*.

Genus **Saccinobaculus** Cleveland. Elongate to spherical; 4 (8 or 12) flagella; axostyle large, paddle-like, deeply stained with Heidenhain, undulates, and serves for locomotion; parasitic.

S. ambloaxostylus C. (Fig. 125, *g*). 65–110 μ by 18–26 μ ; in *Cryptocercus punctulatus*.

Family 6 Trichomonadidae

With both axial organellae and an undulating membrane.

Genus **Trichomonas** Donné (*Ditrichomonas* Cutler). Pyriform; 4 anterior flagella; another flagellum along the margin of undulating membrane; costa along the base of the membrane; axostyle projects beyond the posterior end of body; cysts observed in forms inhabiting the animal intestines, but not in those living in man; parasitic in gut of vertebrates and invertebrates. Numerous species.

T. hominis (Davaine) (Fig. 126, *a*). 5–18 μ long; in human intestine.

T. elongata Steinberg (*T. buccalis* Goodey et Wellings) (Fig. 126, b). About 10–20 μ long; in human mouth.

T. vaginalis Donné (Fig. 126, c). 10–25 μ long; in human vagina.

T. batrachorum (Perty). Ovoid; 14–18 μ by 6–10 μ ; in frog gut.

T. augusta Alexeieff. Spindle-form; 18–22 μ by 8–14 μ ; in frog gut.

T. linearis Kirby (Fig. 126, d). Elongate, spindle-form; 9–24 μ by 3–8 μ ; in gut of *Orthognathotermes wheeleri*; Panama.

T. termitis (Cutler) (Fig. 126, e). 30–88 μ by 13–57 μ (Imms); in gut of *Archotermopsis wroughtoni*; India.

Genus **Gigantomonas** Dogiel (*Myxomonas* D.). Somewhat similar to *Trichomonas*, but much larger; 3 short flagella and a very long flagellum; axostyle large; undulating membrane well developed; parasitic.

G. herculea D. (Fig. 126, f). 60–75 μ by 30–35 μ ; in gut of *Hodotermes mossambicus*. *Myxomonas polymorpha* D. (g) reported from the same host appears to be a degenerating specimen.

Genus **Tritrichomonas** Kofoid. Similar to *Trichomonas* in appearance and structure; but 3 anterior flagella; parasitic.

T. brevicollis Kirby (Fig. 126, h). Ovoid; undulating membrane curved around end; 10–17 μ by 4–8 μ ; in gut of *Kalotermes brevicollis*; Panama.

T. foetus (Riedmüller). Pathogenic; in genitalia of cattle; similar to *Trichomonas vaginalis*; but 3 anterior flagella; body about 15 μ by 5 μ ; transmission by sexual act, from cow to bull or bull to cow; in infected cow conception temporarily or permanently suspended or death of foetus occurs.

T. fecalis Cleveland. 5 μ by 4 μ to 12 μ by 6 μ ; average dimensions 8.5 μ by 5.7 μ ; axostyle long, protruding 1/3–1/2 the body length from the posterior end; of 3 flagella, one is longer and less active than the other two; in the faeces of man. Its remarkable adaptability observed by Cleveland was noted elsewhere (p. 28).

Genus **Tricercomitus** Kirby. Small; 3 anterior flagella; a long trailing flagellum, adhering to body; nucleus anterior, without endosome; blepharoplast large, with a parabasal body and an axial filament; parasitic.

T. termopsidis K. (Fig. 126, i, j). 4–12 μ by 2–3 μ ; anterior flagella 6–20 μ long; trailing flagellum 19–65 μ long; in gut of *Zootermopsis angusticollis*, *Z. nevadensis* and *Z. laticeps*; California and Arizona.

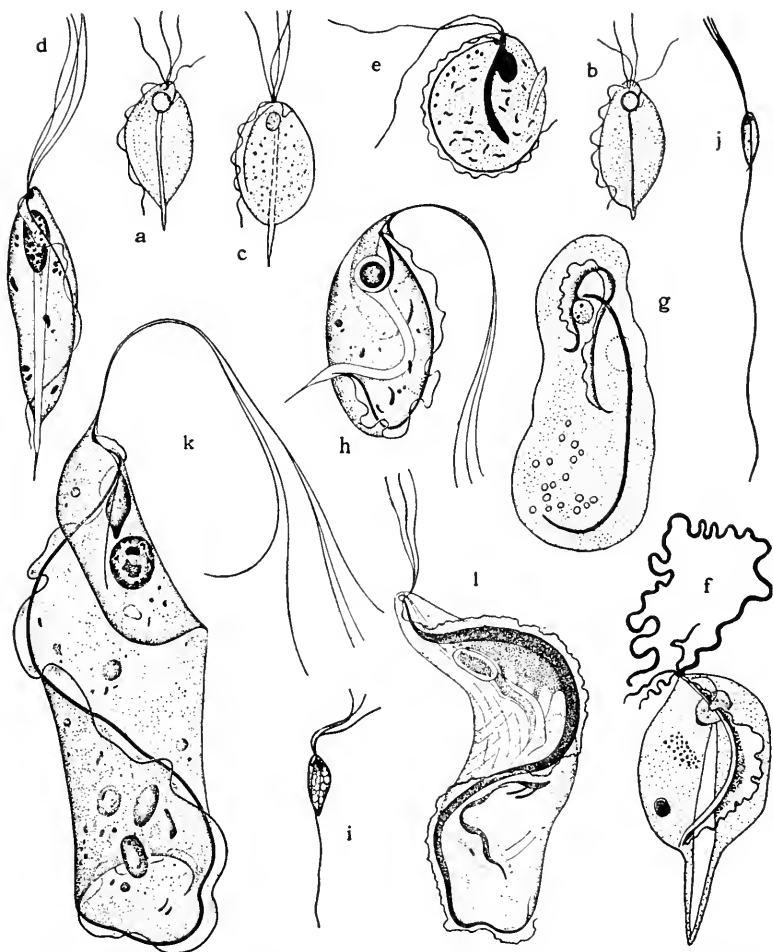


FIG. 126. a, *Trichomonas hominis*, $\times 1070$ (Kudo); b, *T. elongata*, $\times 1070$ (Kudo); c, *T. vaginalis*, $\times 870$ (Wenyon); d, *T. linearis*, $\times 2000$ (Kirby); e, *T. termitis*, $\times 630$ (Cutler); f, *Gigantomonas herculea*, $\times 530$ (Dogiel); g, a degenerating form, $\times 400$ (Dogiel); h, *Tritrichomonas brevicollis*, $\times 2000$ (Kirby); i, j, *Tricercomitus termopsidis*, $\times 890$ (Kirby); k, *Pentatrichomonas scroa*, $\times 2000$ (Kirby); l, *Pseudotrypanosoma giganteum*, $\times 580$ (Kirby).

Genus **Pentatrichomonas** Chatterjee. 5 anterior flagella; axostyle very slightly developed; parabasal body fusiform; nucleus at some distance from anterior end; parasitic.

P. scroa Kirby (Fig. 126, *k*). 18–45 μ by 6–15 μ ; in *Kaloterme* *dudleyi* and *K. longicollis*; Panama.

Genus **Pseudotrypanosoma** Grassi. Large, elongate; 3 anterior flagella; undulating membrane; slender axostyle; costa conspicuous; band-like structure between blepharoplast and nucleus; striae near body surface; parabasal body long; parasitic.

P. giganteum G. (Fig. 126, *l*). 55–111 μ long (Grassi); 145–205 μ by 20–40 μ ; anterior flagella about 30 μ long (Kirby); cytostome not observed; in gut of *Porotermes adamsoni* and *P. grandis*; Australia.

Suborder 2 Diplomonadina

The suborder consists of a number of binucleate flagellates possessing bilateral symmetry.

Family Hexamitidae Kent

Genus **Hexamita** Dujardin (*Octomitus* Prowazek). Pyriform; 2 nuclei at anterior pole; 6 anterior and 2 posterior flagella; 2 axostyles; 1–2 contractile vacuoles; cytostome obscure; endoplasm with refractile granules; encystment; in stagnant water or parasitic.

H. inflata D. (Fig. 127, *a*). Broadly oval; posterior end truncate; 13–25 μ by 9–15 μ ; in stagnant water.

H. intestinalis D. (Fig. 127, *b, c*). 10–16 μ long; in intestine of frogs, also in midgut of *Trutta fario* and in rectum of *Motella tricirrata* and *M. mustela* in European waters.

H. salmonis (Moore) (Fig. 127, *d*). 10–12 μ by 6–8 μ ; in intestine of various species of trout and salmon; schizogony in epithelium of pyloric caeca and intestine; cysts; pathogenic to young host fish (Davis, 1925).

H. periplanetae (Bělař) In gut of cockroaches.

H. cryptocerci Cleveland (Fig. 127, *e*). 8–13 μ by 4–5.5 μ ; in *Cryptocercus punctulatus*.

Genus **Giardia** Kunstler (*Lambli*a Blanchard). Pyriform; bilaterally symmetrical; dorsal side convex; ventral side with sucking disc at anterior region; 8 flagella; 4 from margin of sucking disc; 2 from middle part and 2 from posterior end of body; parasites in intestine of various vertebrates. Several species.

G. intestinalis (Lambl) (Fig. 127, *f–h*). 10–20 μ by 6–10 μ ; commensal in human intestine.

G. muris (Grassi). 7–13 μ by 5–10 μ ; in intestine of mice and rats.

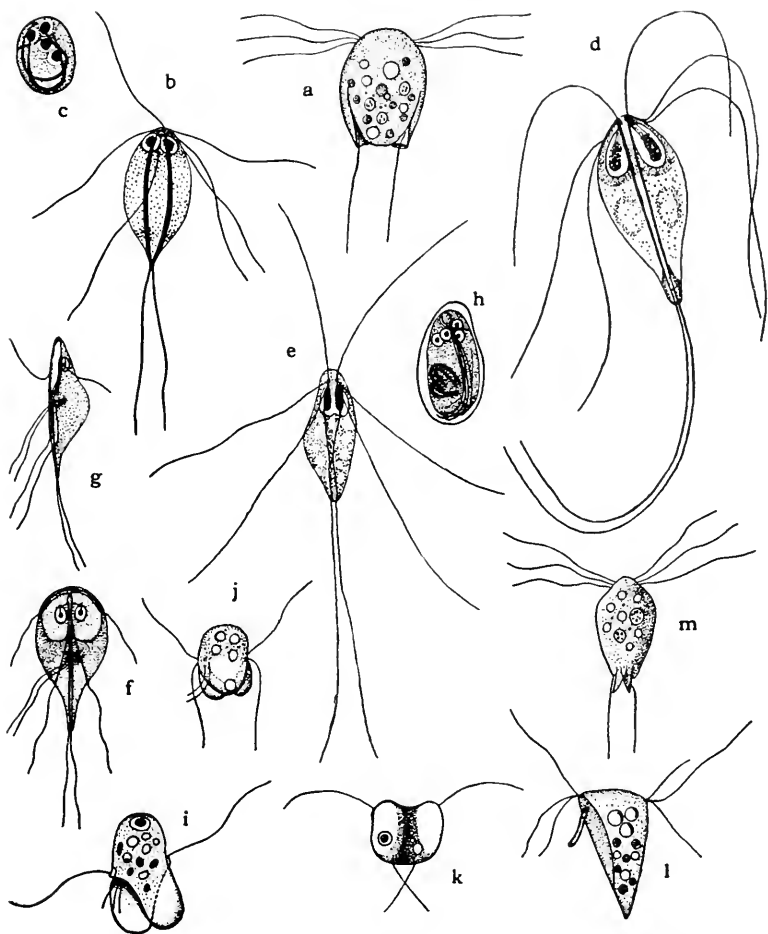


FIG. 127. a, *Hexamita inflata*, $\times 690$ (Klebs); b, c, *H. intestinalis*, $\times 1600$ (Alexeieff); d, *H. salmonis*, $\times 2100$ (Davis); e, *H. cryptocerci*, $\times 1600$ (Cleveland); f-h, *Giardia intestinalis*, $\times 1070$ (Kofoid and Swezy); i, *Trepomonas agilis*, $\times 1070$ (Klebs); j, *T. rotans*, $\times 710$ (Lemmermann); k, *Gyromonas ambulans*, $\times 530$ (Seligo); l, *Trigonomonas compressa*, $\times 490$ (Klebs); m, *Urophagus rostratus*, $\times 800$ (Klebs).

Genus **Trepomonas** Dujardin. Free-swimming; flattened; more or less rounded; cytosomal grooves on posterior half, one on each side; 8 flagella (one long and 3 short flagella on each side) arise from anterior margin of groove; at anterior end there is a horse-

shoe-like structure, in which two nuclei are located; fresh water, parasitic, or coprozoic.

T. agilis D. (Fig. 127, *i*). More or less ovoid; 7–30 μ long; 1 long and 3 short flagella on each side; rotation movement; stagnant water; also reported from intestine of Amphibians.

T. rotans Klebs (Fig. 127, *j*). Broadly oval; posterior half highly flattened; 2 long and 2 short flagella on each of 2 cytostomes; stagnant water.

Genus **Gyromonas** Seligo. Free-swimming; small; form constant, flattened; slightly spirally coiled; 4 flagella at anterior end; cytostome not observed; fresh water.

G. ambulans S. (Fig. 127, *k*). Rounded; 8–15 μ long; standing water.

Genus **Trigonomonas** Klebs. Free-swimming; pyriform; plastic; cytostome on either side, from anterior margin of which arise 3 flagella; flagella 6 in all; 2 nuclei situated near anterior end; movement rotation; holozoic; fresh water.

T. compressa K. (Fig. 127, *l*). 24–33 μ by 10–16 μ ; flagella of different length; standing water.

Genus **Urophagus** Klebs. Somewhat similar to *Hexamita*; but a single cytostome; 2 moveable posterior processes; holozoic; stagnant water.

U. rostratus (Stein) (Fig. 127, *m*). Spindle-form; 16–25 μ by 6–12 μ .

Suborder 3 **Polymonadina**

This group includes forms which inhabit the intestine of various species of termites, most probably as symbionts. The majority are multinucleate. Each nucleus gives rise to a basal body (from which flagella extend), a parabasal body, and an axial filament. Janicki called this complex a *karyomastigont*, and the other type of complex which does not contain a nucleus *akaryomastigont*.

Genus **Calonympha** Foà. Body rounded; large; numerous long flagella arise from anterior region; nuclei arranged near insertion points of flagella; with karyomastigonts or akaryomastigonts; axial filaments form a bundle; in termite gut.

C. grassi F. (Fig. 128, *a*). In *Cryptotermes grassii*; 69–90 μ long.

Genus **Stephanonympha** Janicki. Oval, but plastic; pellicle sculptured with foreign bodies; numerous nuclei spirally arranged around anterior end; in termite gut.

S. nelumbium Kirby (Fig. 128, b). 45μ by 27μ ; in *Cryptotermes hermsi*.

Genus **Microrhopalodina** Grassi et Foà (*Proboscidiella* Kofoid et Swezy). One to many nuclei, each in a karyomastigont com-

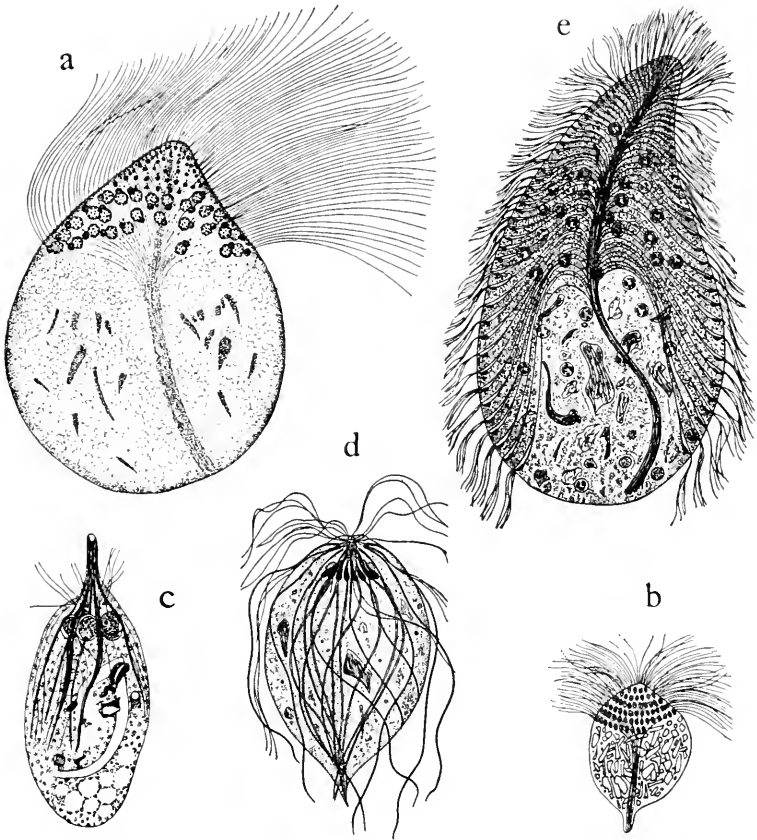


FIG. 128. a, *Calonympha grassii*, $\times 900$ (Janicki); b, *Stephanonympha nelumbium*, $\times 400$ (Kirby); c, *Microrhopalodina multinucleata*, $\times 440$ (Kofoid and Swezy); d, *Coronympha clevelandi*, $\times 1000$ (Kirby); e, *Snyderella tabogae*, $\times 350$ (Kirby).

plex; a single extensible and retractile rostellum; binary fission; in termite gut.

M. multinucleata (Kofoid et Swezy) (Fig. 128, c). $25\text{--}160\mu$ long; in *Kalotermes nocens*.

M. occidentis (Lewis). $26\text{--}133\mu$ by $11\text{--}80\mu$; average number of

nuclei 5.5; about 23 per cent uninucleate; in *Kaloterms occidentis*.

Genus **Coronympha** Kirby. Pyriform with 16 nuclei, arranged in a single circle in anterior region; each nucleus center of a karyomastigont; in termite gut.

C. clevelandi K. (Fig. 128, *d*). 25–53 μ by 18–46 μ , in *Kaloterms clevelandi*; Panama.

Genus **Snyderella** Kirby. Numerous nuclei scattered through cytoplasm; akaryomastigonts close together and extend through greater part of peripheral region; axial filaments in bundle; in termite gut.

S. tabogae K. (Fig. 128, *e*). Pyriform; rounded posteriorly; bluntly conical anteriorly; 77–172 μ by 53–97 μ ; in *Kaloterms longicollis*; Panama.

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CHAPTER 15

Order 4 **Hypermastigina** Grassi

ALL members of this order are inhabitants of the alimentary canal of the termite or other insects. The cytoplasmic organization is of high complexity, although there is only a single nucleus. Flagella are numerous and have their origin in blepharoplasts located at the anterior region of the body. In some species, it has been established by Cleveland that there exists a true symbiotic relationship between the host insects and the protozoans (p. 24). Method of nutrition is either holozoic or saprozoic (parasitic). No cytostome has been detected and bits of wood, starch grains, and other food materials, are taken in by means of pseudopodia.

Asexual reproduction is by longitudinal fission; multiple division has also been noted in some species under certain conditions, while sexual reproduction has not been observed. Encystment occurs in some genera of Lophomonadidae and certain species inhabiting wood-roaches, in which moulting of the host insect leads to encystment. Because of the peculiarity and complexity of their structures and also of their common occurrence in termites, the Hypermastigina have in recent years been frequently studied.

Body without segmented appearance

Flagella in spiral rows. Family 1 Holomastigotidae

Flagella not arranged in spiral rows

Flagella in one or more anterior tufts

1 tuft of flagella. Family 2 Lophomonadidae (p. 280)

2 tufts of flagella. Family 3 Hoplonymphidae (p. 282)

4 tufts of flagella. Family 4 Staurojoeninidae (p. 284)

Several tufts (loriculae). Family 5 Kofoidiidae (p. 284)

Flagella not arranged in tufts

Posterior part without flagella.

. Family 6 Trichonymphidae (p. 284)

Flagella over entire body. Family 7 Eucomonymphidae (p. 286)

Body with segmented appearance. Family 8 Teratonymphidae (p. 287)

Family 1 **Holomastigotidae** Janicki

Flagella are arranged in spiral rows; posterior region may be without flagella; the "anterior body" surrounds, or occurs near,

the nucleus; reproduction by longitudinal division; inhabitants of termite gut.

Genus **Holomastigotes** Grassi. Body small; spindle-shaped; few spiral rows reach from anterior to posterior end; nucleus anterior, surrounded by a mass of dense cytoplasm; nutrition by absorption of fluid material; in termite gut.

H. elongatum G. (Fig. 129, a). In gut of *Reticulitermes lucifugus*, *R. speratus*, *R. flaviceps*, and *Macrohodotermes mossambicus*; up to 70μ by 24μ (Grassi).

Genus **Holomastigotoides** Grassi et Foà. Large; spindle-shaped; spiral rows of flagella as in the last genus, but more numerous (12–40 rows); a mass of dense cytoplasm surrounds ovoid nucleus; in termite gut.

H. hartmanni Koidzumi (Fig. 129, b). $50\text{--}140\mu$ long; in *Coptotermes formosanus*.

Genus **Spirotrichonympha** Grassi. Moderately large; elongate pyriform; flagella deeply embedded in cytoplasm in anterior region, arising from 1-several spiral bands; mass of dense cytoplasm conical and its base indistinct; nucleus spherical; in termite gut.

S. leidyi Koidzumi (Fig. 129, c). In *Coptotermes formosanus*; $15\text{--}50\mu$ by $8\text{--}30\mu$.

S. pulchella Brown (Fig. 129, d). $36\text{--}42\mu$ by $14\text{--}16\mu$; in *Reticulitermes hageni*.

S. polygyra Cupp. (Fig. 58). In *Kaloterms simplicicornis*; $63\text{--}112\mu$ by $25\text{--}60\mu$; four flagellar bands.

Genus **Spirotrichonymphella** Grassi. Small; without spiral ridges; flagella longer; not wood-feeding; in termite gut.

S. pudibunda G. In *Porotermes adamsoni*; Australia. Multiple fusion (Sutherland).

Genus **Microspirotrichonympha** Koidzumi (*Spironympha* Koidzumi). Small, surface not ridged; spiral rows of flagella only on anterior half; a tubular structure between nucleus and anterior extremity; a mass of dense cytoplasm surrounds nucleus; with or without axial rod; in termite gut.

M. porteri K. (Fig. 129, e). In *Leucotermes flaviceps*; $20\text{--}55\mu$ by $20\text{--}40\mu$.

M. ovalis (Brown) (Fig. 129, f). $36\text{--}48\mu$ by about 40μ ; in *Reticulitermes hesperus*.

Genus **Spirotrichosoma** Sutherland. Pyriform or elongate; be-

low operculum, two deeply staining rods from which flagella arise and which extends posteriorly into 2 spiral flagellar bands; without axostyle; nucleus anterior, median; wood chips always present, but method of feeding unknown; in *Stolotermes victoriensis*; Australia.

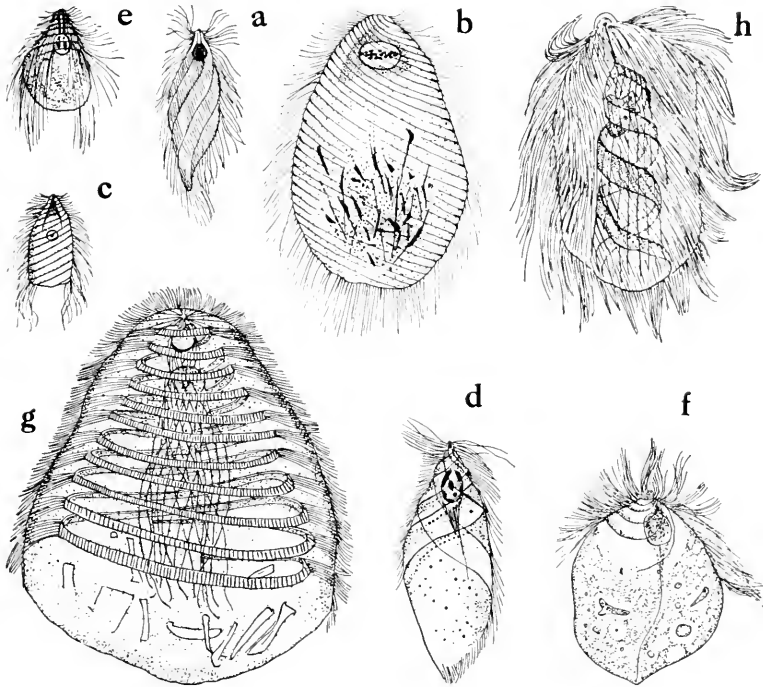


FIG. 129. a, *Holomastigotes elongatum*, $\times 700$ (Koidzumi); b, *Holomastigotoides hartmanni*, $\times 250$ (Koidzumi); c, *Spirotrichonympha leidy*, $\times 400$ (Koidzumi); d, *S. pulchella*, $\times 900$ (Brown); e, *Microspirotrichonympha porteri*, $\times 250$ (Koidzumi); f, *M. oralis*, $\times 600$ (Brown); g, *Macrospironympha xylopletha*, $\times 300$ (Cleveland et al.); h, *Leptospironympha eupora*, $\times 1050$ (Cleveland et al.).

S. capitata S. 97μ by 38μ ; flagellar bands closely spiral, reach posterior end.

Genus **Macrospironympha** Cleveland. Broadly conical; flagella on 2 broad flagellar bands which make 10–12 spiral turns, 2 inner bands; axostyles 36–50 or more; during mitosis nucleus migrates posteriorly; encystment, in which only nucleus and centrioles are

retained, takes place at each ecdysis of host; in *Cryptocercus punctulatus*.

M. xylopletha C. (Fig. 129, *g*). 112–154 μ by 72–127 μ .

Genus **Leptospironympha** Cleveland. Cylindrical; small; flagella on 2 bands winding spirally along body axis; axostyle single, hyaline; nucleus does not migrate posteriorly during division; encystment unknown; in *Cryptocercus punctulatus*.

L. eupora C. (Fig. 129, *h*). 30–38 μ by 18–21 μ .

Family 2 **Lophomonadidae** Kent

Numerous flagella arise from anterior end in a tuft; each flagellum originates in a blepharoplast from which extends inward an axostylar filament; nucleus anterior, surrounded by a funnel-shaped space formed by filaments; no cytostome; parabasal body; nutrition holozoic or parasitic; reproduction by binary or multiple fission; encystment common; sexual reproduction unknown; in cockroaches and termite guts.

Genus **Lophomonas** Stein. Ovoid or elongate; small; a vesicular nucleus anterior; cysts common; in colon of cockroaches.

L. blattarum S. (Figs. 23; 59; 66; 130, *a-e*). Small, pyriform, but plastic; bundle of axostylar filaments may project beyond posterior margin; active swimming movements; binary or multiple fission; 25–30 μ long; holozoic in colon of cockroaches; widely distributed.

L. striata Bütschli (Fig. 130, *f-h*). Elongate spindle; surface with obliquely arranged needle-like structures which some investigators believe to be a protophytan (to which Grassé gave the name, *Fusiformis lophomonadis*); bundle of axial filaments short, never protruding; movement sluggish; cyst spherical with needle-like structures; in same habitat as the last species.

Genus **Eulophomonas** Grassi et Foà. Similar to *Lophomonas*, but flagella vary from 5–15 or a little more in number; in termite gut.

E. kalotermitis Grassi. In *Kalotermes flavicollis*; this flagellate has not been observed by other workers.

Genus **Prolophomonas** Cleveland. Similar to *Eulophomonas*; established since *Eulophomonas* had not been seen by recent workers; would become synonym “if *Eulophomonas* can be found in *K. flavicollis*” (Cleveland).

P. tocopola C. (Fig. 130, *i*). 14–19 μ by 12–15 μ ; in *Cryptocercus punctulatus*.

Genus **Joenia** Grassi. Ellipsoidal; anterior portion capable of forming pseudopodia; flagellar tufts in part directed posteriorly; surface covered by numerous immobile short filamentous processes, which some hold to be symbiotic bacteria; nucleus spherical

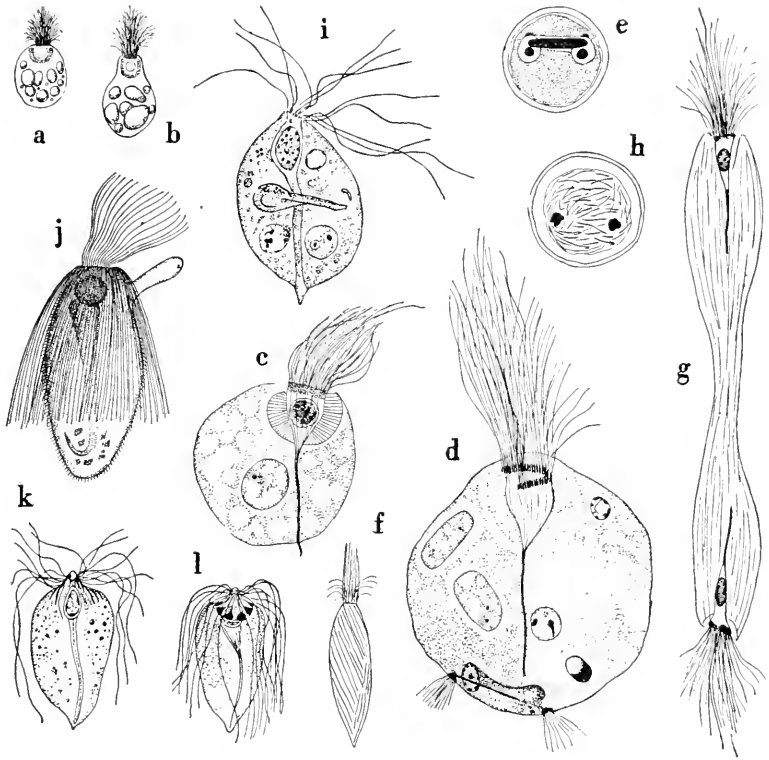


FIG. 130. a–e, *Lophomonas blattarum* (a, b, in life, $\times 320$; c, d, stained specimens; e, cyst, $\times 1150$) (Kudo); f–h, *L. striata* (f, in life, $\times 320$; g, h, stained individuals, $\times 1150$) (Kudo); i, *Prolophomonas tocopola*, $\times 1200$ (Cleveland et al.); j, *Joenia annectens* (Grassi and Foà); k, *Microjoenia pyriformis*, $\times 920$ (Brown); l, *Torquenympha octoplus*, $\times 920$ (Brown).

anterior; posterior to it a conspicuous axostyle composed of numerous axial filaments, a parabasal apparatus surrounding it; bits of wood used as food; in termite gut.

J. annectens G. (Fig. 130, j). In *Kaloterme flavicollis*.

Genus **Joenia** Grassi. More complex in structure than that of

Joenia; flagella inserted at anterior end in a semi-circle; parabasal bodies 2 elongated curved rods; feeding on wood fragments.

J. pulchella G. In *Porotermes adamsoni*.

Genus **Joenopsis** Cutler. Oval; large; a horseshoe-shaped pillar at anterior end, flagella arising from it; some directed anteriorly, others posteriorly; parabasal bodies long rods; a strong axostyle; feeding on bits of wood; in termite gut.

J. polytricha C. In *Archotermopsis wroughtoni*; 95–129 μ long.

Genus **Microjoenia** Grassi. Small, pyriform; anterior end flattened; flagella arranged in longitudinal rows; axostyle; parabasal body simple; in termite gut.

M. pyriformis Brown (Fig. 130, *k*). 44–52 μ by 24–30 μ ; in *Reticulitermes hageni*.

Genus **Mesojoenia** Grassi. Large; flagellar tuft spread over a wide area; distinct axostyle, bent at posterior end; 2 parabasal bodies; in termite gut.

M. decipiens G. In *Kaloterms flavicollis*.

Genus **Torquenympha** Brown. Small; pyriform or top-form; axostyle; radially symmetrical; 8 radially arranged parabasal bodies; nucleus anterior; in termite gut.

T. octoplus B. (Fig. 130, *l*). 15–26 μ by 9–13 μ ; in *Reticulitermes hesperus*.

Family 3 Hoplonymphidae Light

2 flagellar tufts; each arises from a plate near anterior end of slender body which is protected by a highly developed pellicular armor.

Genus **Hoplonympha** Light. Slender fusiform, covered with thick, rigid pellicular armor; each tuft of flagella arises from a plate connected with blepharoplasts at anterior end; nucleus near anterior extremity, more or less triangular in form; in termite gut.

H. natator L. (Fig. 131, *a, b*). 60–120 μ by 5–12 μ ; in *Kaloterms simplicicornis*.

Genus **Barbulanympha** Cleveland. Acorn-shaped; small, narrow, nuclear sleeve between centrioles; number of rows of flagella greater at base; large chromatin granules; numerous (80–350) parabasals; axostylar filaments 80–350; flagella 1500–13,000; different species show different number of chromosomes during mitosis; in gut of *Cryptocercus punctulatus*. Four species.

B. ufalula C. (Figs. 57; 131, *c*). 250–340 μ by 175–275 μ ; 50

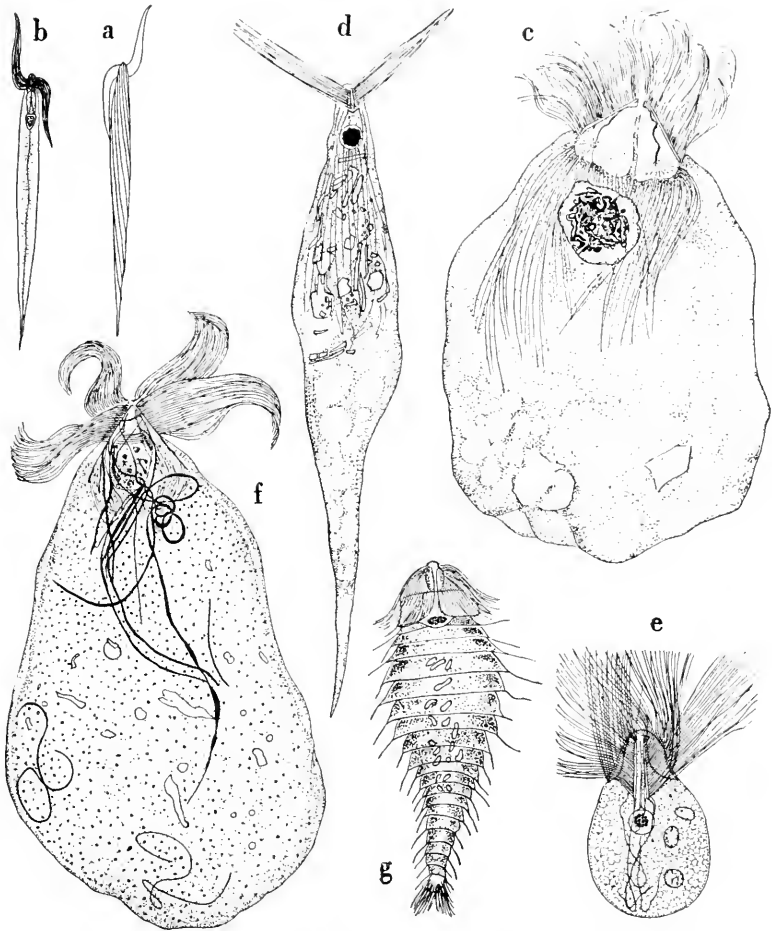


FIG. 131. a, b, *Hoplonympha natator*, $\times 450$ (Light); c, *Barbulonympha ufalula*, $\times 210$ (Cleveland et al.); d, *Urinympha talea*, $\times 350$ (Cleveland et al.); e, *Staurjoenina assimilis*, $\times 200$ (Kirby); f, *Idionympha perissa*, $\times 250$ (Cleveland et al.); g, *Teratonympha mirabilis*, $\times 200$ (Dogiel).

chromosomes; flagellated area $36\text{--}41\mu$ long; centriole $28\text{--}35\mu$ long.

B. laurabuda C. $180\text{--}240\mu$ by $135\text{--}170\mu$; 40 chromosomes; flagellated area $29\text{--}33\mu$ long; $24\text{--}28\mu$ long.

Genus **Rhynchonympha** Cleveland. Elongate; number of flagellar rows same throughout; axial filaments somewhat larger and

longer, about 30; 30 parabasals; 2400 flagella; in *Cryptocercus punctulatus*.

R. tarda C. (Fig. 132, *f*). 130–215 μ by 30–70 μ .

Genus **Urinympha** Cleveland. Narrow, slender; flagellated area, smaller than that of the two genera mentioned above; flagella move as a unit; about 24 axial filaments; 24 parabasals; 600 flagella; in gut of *Cryptocercus punctulatus*.

U. talea C. (Fig. 131, *d*). 75–300 μ by 15–50 μ .

Family 4 Staurojoeninidae Grassi

4 flagellar tufts arise from the anterior end.

Genus **Staurojoenina** Grassi. Pyriform to cylindrical; anterior region conical; nucleus spherical, central; 4 flagellar tufts from anterior end; ingest wood fragments; in termite gut.

S. assimilis Kirby (Fig. 131, *e*). 105–190 μ long; in *Kaloterms minor*.

Genus **Idionympha** Cleveland. Acorn-shaped; axostyles 8–18; fine parabasals grouped in 4 areas; pellicle non-striated; nucleus nearer anterior end than that of *Staurojoenina*; flagellated areas smaller; in gut of *Cryptocercus punctulatus*.

I. perissa C. (Fig. 131, *f*). 160–275 μ by 98–155 μ .

Family 5 Kofoidiidae Light

Flagellar tufts composed of 8–16 loricae (permanently fused bundles of flagella); without either axostyle or parabasal body.

Genus **Kofoidia** Light. Spherical; between oval nucleus and bases of flagellar tufts, there occurs a chromatin collar; wood fragments as food; in termite gut.

K. loridata L. (Fig. 132, *a*, *b*). 60–140 μ in diameter; in *Kaloterms simplicicornis*.

Family 6 Trichonymphidae Kent

The body is divisible into three regions; rostellum with caps, flagellated region behind rostellum and non-flagellated area at posterior end; flagellated area 1/3–2/3 of body length; surface of anterior portion differentiated into 1–2 thick ectoplasmic layers, densely traversed by numerous flagella; an “axial core” or “head organ” at anterior tip; no cytostome; a single nucleus; flagella numerous and long, arranged in longitudinal rows; multiplication by simple longitudinal fission; inhabitants of termites and wood-roach.

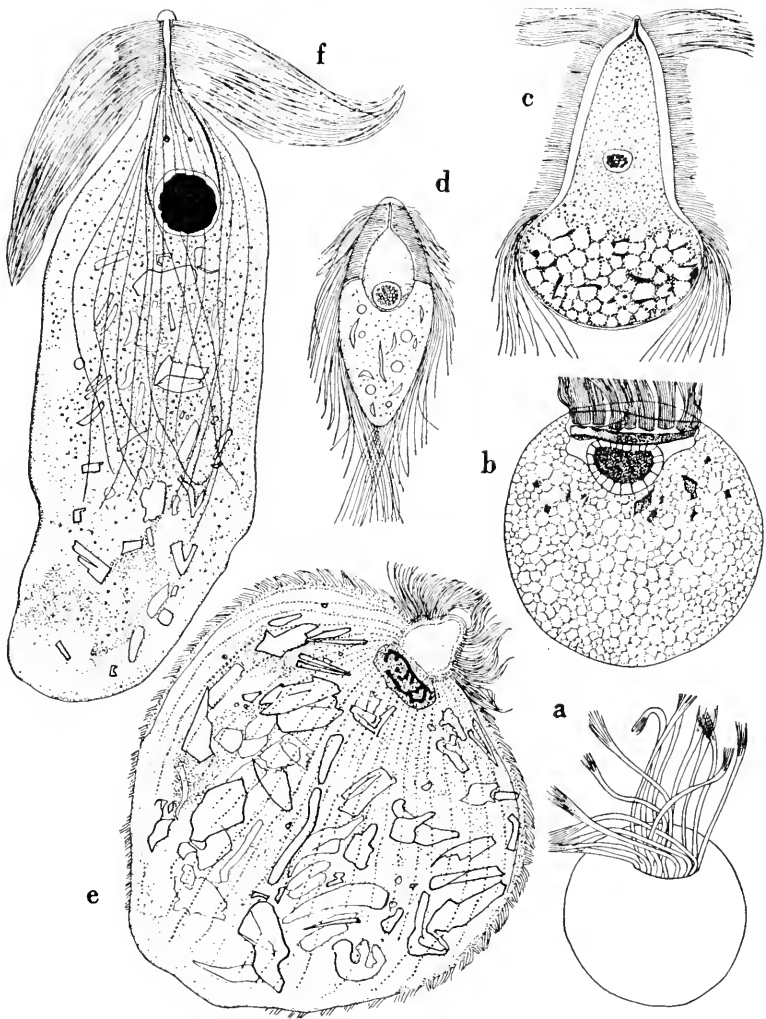


FIG. 132. a, b, *Kofoidia loriculata*, $\times 175$, $\times 300$ (Light); c, *Trichonympha campanula*, $\times 150$ (Kofoid and Swezy); d, *T. agilis*, $\times 410$ (Kirby); e, *Eucomonympha imla*, $\times 350$ (Cleveland et al.); f, *Rhynchonympha tarda*, $\times 350$ (Cleveland et al.).

Genus **Trichonympha** Leidy (*Leidyonella* Frenzel; *Gymnonympha* Dobell; *Leidyopsis* Kofoid et Swezy). Anterior portion consists of nipple and bell, both of which are composed of 2 layers; a distinct axial core; nucleus central; flagella located in longi-

tudinal rows on bell; in termite gut. Many species. Cleveland and his associates (1934) observed that encystment takes place in species inhabiting the wood-roach, *Cryptocercus punctulatus* and that it occurs only at the time of moulting of the host roach, namely once a year.

T. campanula Kofoid et Swezy (Figs. 56; 132, c). 144–313 μ by 57–144 μ ; wood particles are taken in by posterior region by a method of Rumbler's "import" (Cleveland). In *Zootermopsis angusticollis*, *Z. nevadensis* and *Z. laticeps*.

T. agilis Leidy (Fig. 132, d). 55–115 μ by 22–45 μ ; in *Reticulitermes flavipes*, *R. lucifugus*, *R. speratus*, *R. flaviceps*, *R. hesperus*, *R. tibialis*.

T. grandis Cleveland. 190–205 μ by 79–88 μ ; in *Cryptocercus punctulatus*.

Genus **Pseudotrichonympha** Grassi. 2 parts in anterior end as in *Trichonympha*; head organ with a spherical body at its tip and surrounded by a single layer of ectoplasm; bell covered by 2 layers of ectoplasm; nucleus lies freely; body covered by slightly oblique rows of short flagella; in termite gut.

P. grassii Koidzumi. In *Coptotermes formosanus*; spindle-form; 200–300 μ by 50–120 μ .

Genus **Deltotrichonympha** Sutherland. Triangular; with a small dome-shaped "head"; composed of 2 layers; head and neck with long active flagella; body flagella short, arranged in 5 longitudinal rows; flagella absent along posterior margin; nucleus large oval, located in anterior third; cytoplasm with wood chips; in termite gut. One species.

D. operculata S. Up to 230 μ long, 164 μ wide, and about 50 μ thick; in gut of *Mastotermes darwiniensis*; Australia.

Family 7 **Eucomonymphidae** Cleveland

All or most of body covered with flagella that arise from basal granules arranged in nearly longitudinal rows; flagella in 2 different groups, and never in 3 groups as in *Trichonymphidae*; without peri-nuclear arrangement of parabasals.

Genus **Eucomonympha** Cleveland. Body covered with flagella arranged in 2 (longer rostral and shorter post-rostral) zones; rostral tube very broad, filled with hyaline material; nucleus at base of rostrum; in gut of *Cryptocercus punctulatus*.

E. imla C. (Fig. 132, e). 100–165 μ by 48–160 μ ; attached forms more elongate than free individuals.

Family 8 **Teratonymphidae** Koidzumi

Genus **Teratonympha** Koidzumi (*Cyclonympha* Dogiel). Large and elongate; transversely ridged, and presents a metameric appearance; each ridge with a single row of flagella; no cytostome; anterior end complex, containing a nucleus; reproduction by longitudinal fission; in termite gut.

T. mirabilis K. (Fig. 131, g). 200–300 μ or longer by 40–50 μ ; in *Reticulitermes speratus* of Japan.

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Class 2 Sarcodina Bütschli

THE members of this class do not possess any definite pellicle and, therefore, are capable of forming pseudopodia (p. 40). The term 'amoeboid' is often used to describe their appearance. The pseudopodia serve for both locomotion and food-capturing. The peripheral portion of the body shows no structural differentiation in Amoebina, Proteomyxa, and Mycetozoa. Internal and external skeletal structures are variously developed in other orders. Thus, in Testacea and Foraminifera, there is a well-developed test or shell that usually has an aperture, through which the pseudopodia are extruded; in Heliozoa and Radiolaria, skeletons of various forms and materials are developed.

The cytoplasm is, as a rule, differentiated into the ectoplasm and the endoplasm, but this differentiation is not constant. In Radiolaria, there is a perforated membranous 'central capsule' which marks the border line between the two cytoplasmic layers. The endoplasm contains the nuclei, food vacuoles, various granules, and contractile vacuoles. The majority of Sarcodina are uninucleate, but numerous species of Foraminifera and Mycetozoa are multinucleate. In the family Paramoebidae, there occurs a peculiar 'secondary nucleus.'

The Sarcodina are typically holozic, but in a few cases holophytic. Their food organisms are Protozoa, small Metazoa and Protophyta, which present themselves conspicuously in the cytoplasm. One or more contractile vacuoles are invariably present in forms inhabiting the fresh water, but absent in parasitic forms or in those which live in the salt water.

Asexual reproduction is usually by binary (or rarely multiple) fission, budding, or plasmotomy. Definite proof of sexual reproduction has been given in a comparatively small number of species. Encystment is common in the majority of Sarcodina, but is unknown in a few species. The life-cycle has been worked out in some forms and seems to vary among different groups. The young stages are either amoeboid or flagellate, and on this account, it is sometimes very difficult to distinguish the Sarcodina and the Mastigophora. In some forms the mature trophic stage

may show an amoeboid or flagellate phase owing to differences in environmental conditions.

The Sarcodina are divided into two subclasses as follows:

- With lobopodia, rhizopodia, or filopodia Subclass 1 Rhizopoda
 Subclass 2 Actinopoda (p. 356)
 With axopodia

Subclass 1 **Rhizopoda** Siebold

The name Rhizopoda has often been used to designate the entire class, but it is used here for one of the subclasses, which is further subdivided into five orders, as follows:

- Without test or shell
 With radiating pseudopodia Order 1 Proteomyxa
 With rhizopodia; forming plasmodium Order 2 Mycetozoa (p. 296)
 Order 3 Amoebina (p. 304)
 With lobopodia
 With test or shell
 Test single-chambered; chitinous Order 4 Testacea (p. 323)
 Test 1- to many-chambered; calcareous Order 5 Foraminifera (p. 344)

Order 1 **Proteomyxa** Lankester

A number of incompletely known Rhizopods are placed in this group. The pseudopodia are filopodia which often branch or anastomose with one another. In this respect the Proteomyxa show affinity to the Mycetozoa. Flagellate swimmers and encystment occur commonly. The majority of Proteomyxa lead parasitic life in algae or higher plants in fresh or salt water.

Pseudoplasmodium-formation Family 1 Labyrinthulidae

Solitary and Heliozoa-like

With flagellate swimmers . . . Family 2 Pseudosporidae (p. 290)

Without flagellate swimmers. Family 3 Vampyrellidae (p. 290)

Family 1 **Labyrinthulidae** Haeckel

Small fusiform protoplasmic masses are grouped in network of sparingly branched and anastomosing filopodia; individuals encyst independently; with or without flagellate stages.

Genus **Labyrinthula** Cienkowski. Minute forms feeding on various species of algae in fresh or salt water; often brightly colored due to the chlorophyll bodies taken in as food.

L. cienkowskii Zopf (Fig. 133, *a*). Attacks *Vaucheria* in fresh water.

L. sp. Renn. Renn (1934, 1936) found in the diseased leaf tissue of the eel-grass, *Zostera marina*, whose leaves showed 'spotting and darkening,' a species of *Labyrinthula*; fusiform with terminal, often branching, filopods; frequently in network by association of many individuals; infected host cell is completely destroyed; Atlantic coast.

Genus **Labyrinthomyxa** Duboseq. Body fusiform; amoeboid and flagellate phases, variable in size; flagellate stage penetrates the host cell membrane; in plants.

L. sauvageau D. (Fig. 133, *b-e*). Fusiform body 7–11 μ long; pseudoplasmodium-formation; amoeboid stage 2.5–14 μ long; flagellate stage 7–18 μ long; parasitic in *Laminaria lejolisii* at Roseoff, France.

Family 2 **Pseudosporidae** Berlese

Genus **Pseudospora** Cienkowski. Body minute; parasitic in algae and Mastigophora (including Volvocidae); organism nourishes itself on host protoplasm, grows and multiplies into a number of smaller individuals, by repeated division; the latter biflagellate, seek a new host, and transform themselves into amoeboid stage; encystment common.

P. volvocis C. (Fig. 133, *f, g*). Heliozoan form about 12–30 μ in diameter; pseudopodia radiating; cysts about 25 μ in diameter; in species of *Volvox*.

P. parasitica C. Attacks *Spirogyra* and allied algae.

P. eudorini Roskin. Heliozoan forms 10–12 μ in diameter; radiating pseudopodia 2–3 times longer; amoeboid within host colony; cysts 15 μ in diameter; in *Eudorina elegans*.

Genus **Protomonas** Cienkowski. Body irregularly rounded with radiating filopodia; food consists of starch grains; division into biflagellate swimmers which become amoeboid and unite to form pseudoplasmodium; fresh or salt water.

P. amyli C. (Fig. 133, *h-j*). In fresh water.

Family 3 **Vampyrellidae** Doflein

Filopodia radiate from all sides or formed from a limited area; flagellate swimmers do not occur; the organism is able to bore through the cellulose membrane of various algae and feeds on

protoplasmic contents; body often reddish because of the formation of carotin; multinucleate; multiplication in encysted stage into uni- or multi-nucleate bodies; cysts often also reddish.

Genus **Vampyrella** Cienkowski. Heliozoa-like; endoplasm

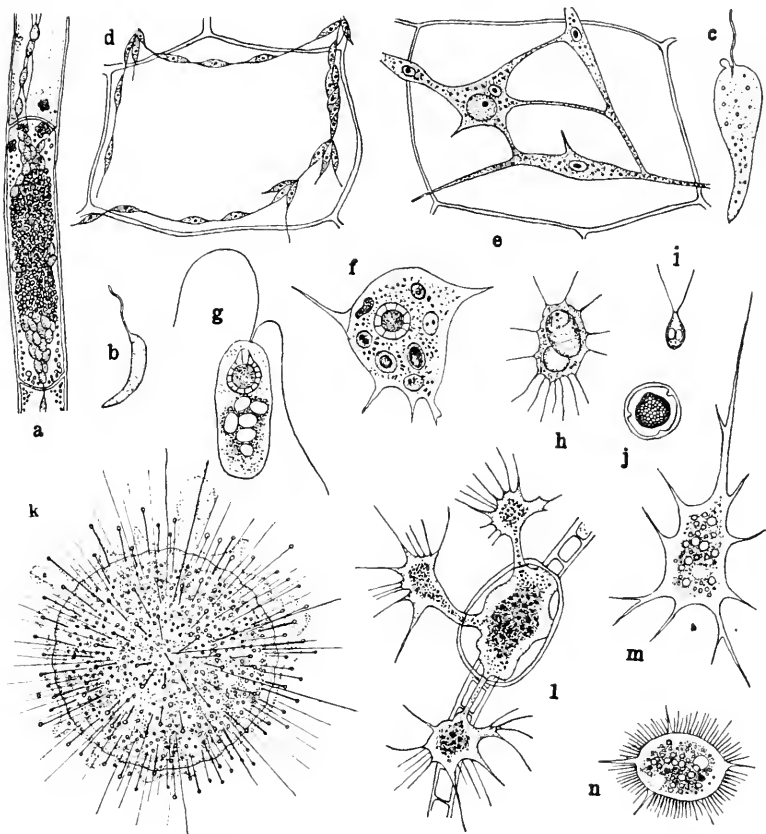


FIG. 133. a, *Labyrinthula cienkowskii*, $\times 200$ (Doflein); b-e, *Labyrinthomyxa sawageaui* (b, c, flagellate forms, $\times 100$; d, e, amoeboid forms, $\times 500$) (Duboseq); f, g, *Pseudospora volvocis*, $\times 670$ (Robertson); h-j, *Protomonas amyli* (Zopf); k, l, *Vampyrella lateritia*, $\times 530$ (k (Leidy), l (Doflein)); m, n, *Nuclearia delicatula*, $\times 300$ (Cash).

vacuolated or granulated, with carotin granules; numerous vesicular nuclei and contractile vacuoles; multinucleate cysts, sometimes with stalk; $50-700\mu$ in diameter. Several species.

V. lateritia (Fresenius) (Fig. 133, k, l). Spherical; orange-red

except hyaline ectoplasm; feeds on *Spirogyra* and other algae in fresh water. On coming in contact with an alga, it often travels along it and sometimes breaks it at joints, or pierces individual cell and extracts chlorophyll bodies by means of pseudopodia; multiplication in encysted condition; $30\text{--}40\mu$ in diameter.

Genus **Nuclearia** Cienkowski. Subspherical, with sharply pointed fine radiating pseudopodia; actively moving forms vary in shape; with or without a mucous envelope; with one or many nuclei; fresh water.

N. delicatula C. (Fig. 133, *m, n*). Multinucleate; bacteria often adhering to gelatinous envelope; up to 60μ in diameter.

N. simplex C. Uninucleate; 30μ in diameter.

Genus **Arachnula** Cienkowski. Body irregularly chain-form with filopodia extending from ends of branches; numerous nuclei and contractile vacuoles; feeds on diatoms and other micro-organisms.

A. impatiens C. (Fig. 134, *a*). $40\text{--}350\mu$ in diameter.

Genus **Chlamydomyxa** Archer. Body spheroidal; ectoplasm and endoplasm well differentiated; endoplasm often green-colored due to the presence of green spherules; numerous vesicular nuclei; 1-2 contractile vacuoles; secretion of an envelope around the body is followed by multiplication into numerous secondary cysts; cyst wall cellulose; in sphagnum swamp.

C. montana Lankester (Fig. 134, *b, c*). Rounded or ovoid; cytoplasm colored; about 50μ in diameter; when moving, elongate with extremely fine pseudopodia which are straight or slightly curved and which are capable of movement from side to side; non-contractile vacuoles at bases of grouped pseudopods; in active individual there is a constant movement of minute fusiform bodies (function?); when extended $100\text{--}150\mu$ long; total length 300μ or more; fresh water among vegetation.

Genus **Rhizoplasma** Verworn. Spherical or sausage-shaped; with anastomosing filopodia; orange-red; with a few nuclei.

R. kaiserii V. (Fig. 134, *d*). Contracted form 0.5-1 mm. in diameter; with 1-3 nuclei; pseudopodia up to 3 cm. long; extended body up to 10 mm. long; originally described from Red Sea.

Genus **Chondropus** Greeff. Spherical to oval; peripheral portion transparent but often yellowish; endoplasm filled with green, yellow, brown bodies; neither nucleus nor contractile vacuoles

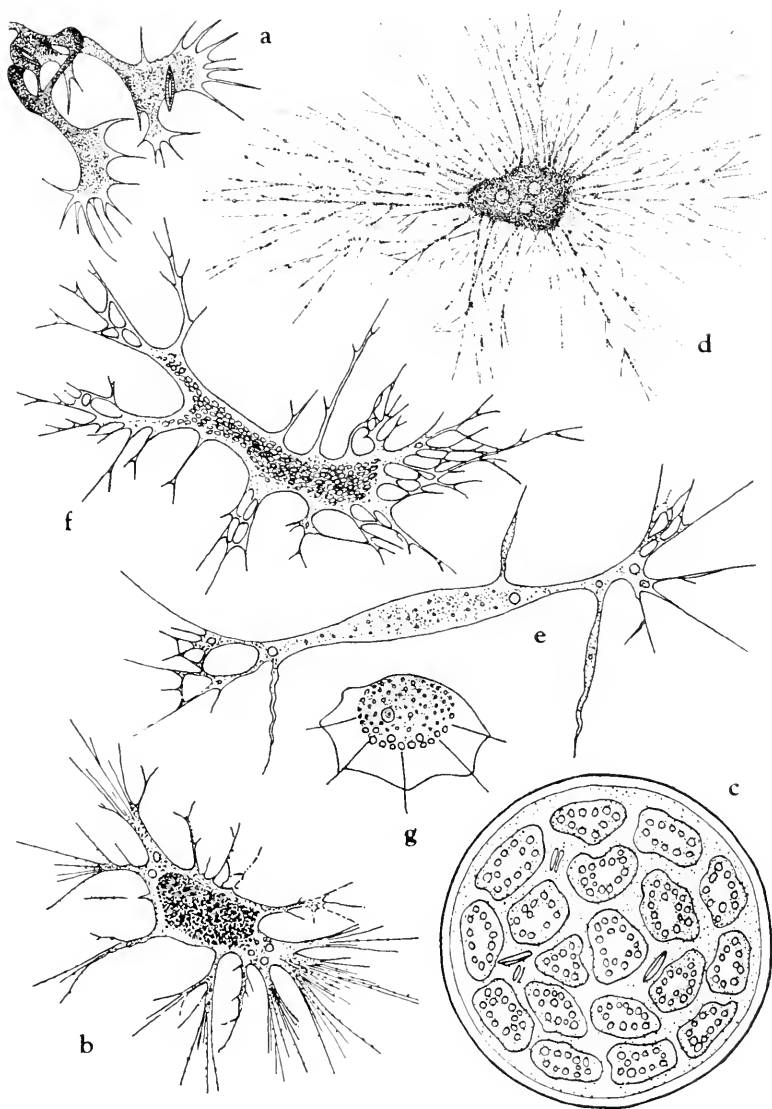


FIG. 134. a, *Arachnula impatiens*, $\times 670$ (Dobell); b, c, *Chlamydomyxa montana*: b, $\times 270$ (Cash); c, $\times 530$ (Penard); d, *Rhizoplasma kaiseri*, $\times 30?$ (Verworn); e, *Biomyxa vagans*, $\times 200$ (Cash); f, *Penardia mutabilis*, $\times 200$ (Cash); g, *Hyalodiscus rubicundus*, $\times 370$ (Penard).

observed; pseudopods straight, fine, often branched; small pearl-like bodies on body surface and pseudopodia.

C. viridis G. Average diameter 35–45 μ ; fresh water among algae.

Genus **Biomyxa** Leidy (*Gymnophrys* Cienkowski). Body form inconstant; initial form spherical; cytoplasm colorless, finely granulated, capable of expanding and extending in any direction, and of projecting filopodia which freely branch and anastomose; cytoplasmic movement active throughout; numerous small contractile vacuoles in body and pseudopodia; with one or more nuclei.

B. vagans L. (Fig. 134, e). Main part, of various forms; size varies greatly; in sphagnum swamps, bog-water, etc.

B. cometa (C.). Subspherical or irregularly ellipsoidal; pseudopodia small in number, formed from 2 or more points; body 35–40 μ , or up to 80 μ or more; pseudopodia 400 μ long or longer. Cienkowski maintained that this was a 'moneran.'

Genus **Penardia** Cash. When inactive rounded or ovoid; at other times expanded; exceedingly mobile during progression; endoplasm chlorophyll-green with a pale marginal zone; filopodia, branching and anastomosing, colorless; nucleus inconspicuous; one or more contractile vacuoles, small; fresh water.

P. mutabilis C. (Fig. 134, f). Resting form 90–100 μ in diameter; extended forms (including Pseudopodia) 300–400 μ long.

Genus **Hyalodiscus** Hertwig et Lesser. Discoid, though outline varies; endoplasm reddish, often vacuolated and sometimes shows filamentous projections reaching body surface; a single nucleus; ectoplasmic band of varying width surrounds the body completely; closely allied to Vampyrella; fresh water.

H. rubicundus H. et L. (Fig. 134, g). 50–80 μ by about 30 μ ; polymorphic; when its progress during movement is interrupted by an object, the body doubles back upon itself, and will move on in some other direction; freshwater ponds among surface vegetation.

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CHAPTER 17

Order 2 **Mycetozoa** de Bary

THE Mycetozoa had been considered to be closely related to fungi, being known as Myxomycetes, or Myxogasteres, the 'slime molds.' Through extended studies of their development, de Bary showed that they are more closely related to the Protozoa than to the Protophyta, although they stand undoubtedly on the border-line between these two groups of microorganisms. The Mycetozoa occur on dead wood or decaying vegetable matter of various kinds.

The most conspicuous part of a mycetozoan is its **plasmodium** which is formed by fusion of several **myxamoebae**, thus producing a large multinucleate body (Fig. 135, *a*). The greater part of the cytoplasm is granulated, although there is a thin layer of hyaline and homogeneous cytoplasm surrounding the whole body. The numerous vesicular nuclei are distributed throughout the granular cytoplasm. Many small contractile vacuoles are present in the peripheral portion of the plasmodium. The nuclei increase in number by division as the body grows; the division seems to be amitotic during the growth period of the plasmodium, but is mitotic prior to the spore-formation. The granulation of the cytoplasm is due to the presence of enormous numbers of granules which in Calcarinea are made up of carbonate of lime. The plasmodium is usually colorless, but sometimes yellow, green, or reddish, because of the numerous droplets of fluid pigment present in the cytoplasm.

The food of Mycetozoa varies among different species. The great majority feed on decaying vegetable matter, but some, such as *Badhamia*, devour living fungi. Thus the Mycetozoa are holozoic or saprozoic in their mode of nutrition. Pepsin has been found in the plasmodium of *Fuligo* and is perhaps secreted into the food vacuoles, into which proteins are taken. The plasmodium of *Badhamia* is said to possess the power of cellulose digestion.

When exposed to unfavorable conditions, such as desiccation, the protoplasmic movement ceases gradually, foreign bodies are extruded, and the whole plasmodium becomes divided into numerous **sclerotia** or cysts, each containing 10–20 nuclei and

being surrounded by a resistant wall (b). These cysts may live as long as three years. Upon return of favorable conditions, the contents of the sclerotia germinate, fuse together, and thus again produce plasmodia (c-e).

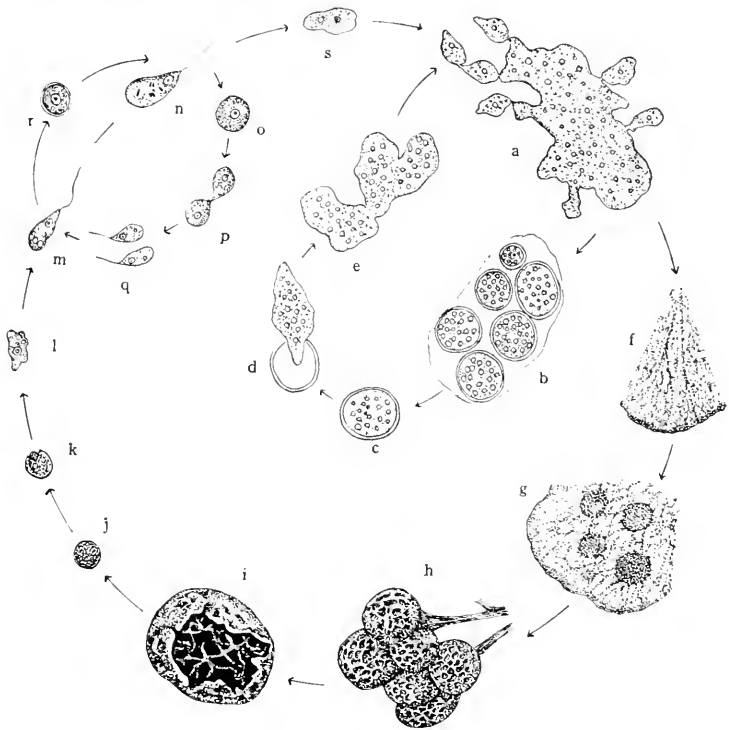


FIG. 135. The life-cycle of the endosporous mycetozoan (de Bary, Lister, and others). a, plasmodium-formation by fusion of numerous myxamoebae; b, c, formation of sclerotium; d, e, germination of sclerotium and formation of plasmodium; f, portion of a plasmodium showing streaming protoplasmic thickenings; g, h, formation of sporangia; i, a sporangium opened, showing capillitium; j, a spore; k, germination of spore; l, myxamoeba; m, n, myxoflagellates; o-q, multiplication of myxoflagellate; r, microcyst; s, myxamoeba. Various magnified.

When lack of food material occurs, the plasmodium undergoes changes and develops **sporangia**. The first indication of this process is the appearance of lobular masses of protoplasm in various parts of the body (f, g). These masses are at first connected with the streaming protoplasmic thickenings, but later become completely segregated into young sporangia. During the

course of sporangium-formation, foreign bodies are thrown out of the body, and around each sporangium there is secreted a wall which, when mature, possesses a wrinkled appearance (*h*). The wall continued down to the substratum as a slender stalk of varying length, and in many genera the end of a stalk spreads into a network over the substratum, which forms the base, **hypothallus**, for the stalk. With these changes the interior of the sporangium becomes penetrated by an anastomosing network, **capillitium**, of flat bands which are continuous with the outer covering (*i*). Soon after the differentiation of these protective and supporting structures, the nuclei divide simultaneously by mitosis and the cytoplasm breaks up into as many small bodies as are nuclei. These uninucleate bodies are the **spores** which measure 3–20 μ in diameter and which soon become covered by a more or less thick cellulose membrane (*j*), variously colored in different species.

The mature sporangium breaks open sooner or later and the spores are carried, and scattered, by the wind. When a spore falls in water, its membrane ruptures, and the protoplasmic contents emerge as an amoebula (*k*, *l*). The amoebula possesses a single vesicular nucleus and contractile vacuoles, and undergoes a typical amoeboid movement. It presently assumes an elongate form and protrudes a flagellum from the nucleated end, thus developing into a **myxoflagellate** (zoospore or swarmer) (*m*, *n*) which undergoes a peculiar dancing movement and is able to form short, pointed pseudopodia from the posterior end. It feeds on bacteria, grows and multiplies by binary fission (*o*–*q*). After a series of division, the myxoflagellate may encyst and becomes a **microcyst** (*r*). When the microcyst germinates, the content develops into a myxamoeba (*s*) which, through fusion with many others, produces the plasmodium mentioned before. This is the life-cycle of a typical endosporous mycetozoon.

In the genus *Ceratiomyxa* in which spores are formed on the surface of **sporophores**, the development is briefly as follows: the plasmodium lives on or in decayed wood and presents a horn-like appearance. The body is covered by a gelatinous hyaline substance, within which the protoplasmic movements may be noted. The protoplasm soon leaves the interior and accumulates at the surface of the mass; at first as a close-set reticulum and then into a mosaic of polygonal cells, each containing a single nucleus.

Each of these cells moves outward at right angles to the surface, still enveloped by the thin hyaline layer, which forms a stalk below. These cells are spores, which become ellipsoid and covered by a membrane when fully formed. The spore is uninucleate at first, but soon becomes tetranucleate. When a spore reaches the water, its contents emerge as an amoebula which divides three times, forming 8 small bodies, each of which develops a flagellum and becomes a myxoflagellate. The remaining part of the development is presumably similar to that of the endosporous form.

An enormous number of mycetozoan genera are known. The order is divided here into two suborders according to Lister.

Spore develops into myxoflagellate; myxamoebae fuse completely and form plasmodium.....Suborder 1 Euplasmodia
 No flagellate stage; myxamoebae grouped prior to spore-formation, but do not fuse to form a true plasmodium.....
Suborder 2 Sorophora (p. 302)

Suborder 1 Euplasmodia Lister

Spores develop within sporangia.....Tribe 1 Endosporeae
 Spores violet or violet-brown.....Legion 1 Amaurosporales
 Sporangia with lime.....Sublegion 1 Calcarinea
 Lime in small granular form.....Family 1 Physaridae

Genus **Badhamia** Berkeley (Fig. 136, *a, b*)

Capillitium, a coarse network with lime throughout.

Genus **Fuligo** Haller (Fig. 136, *c, d*)

Capillitium, a delicate network of threads with vesicular expansions filled with granules of lime.

Lime in crystalline form.....Family 2 Didymiidae

Genus **Didymium** Schrader (Fig. 136, *e, f*)

Lime crystals stellate, distributed over the wall of sporangium.

Sporangia without lime.....Sublegion 2 Amaurochaetinea
 Sporangia stalked.....Family 1 Stemonitidae

Genus **Stemonitis** Gleditsch (Fig. 136, *g, h*)

Sporangium-wall evanescent; capillitium arising from all parts of columella to form a network.

Sporangium combined into aethalium.....
Family 2 Amaurochaetidae

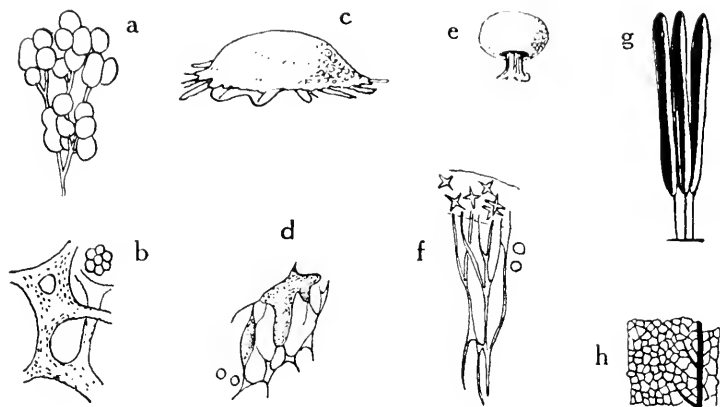


FIG. 136. a, b, *Badhamia utricularis* Berkeley (a, cluster of sporangia, $\times 4$; b, part of capillitium and spore-cluster, $\times 140$) (Lister); c, d, *Fuligo septica* Gmelin (c, a group of sporangia, $\times \frac{1}{3}$; d, part of capillitium and two spores, $\times 120$) (Lister); e, f, *Didymium effusum* Link (e, sporangium, $\times 12$; f, portion of capillitium and wall of sporangium showing the crystals of calcium carbonate and two spores, $\times 200$) (Lister); g, h, *Stemonitis splendens* Rostafinski (g, three sporangia, $\times 2$; h, columella and capillitium, $\times 42$) (Lister).

Genus **Amaurochaete** Rostafinski (Fig. 137, a, b)

With irregularly branching thread-like capillitium.

Spores variously colored, except violet. Legion 2 Lamprosporaes

Capillitium absent or not forming a system of uniform threads. .

. Sublegion 1 Aneminea

Sporangium-wall membranous; with minute round granules. . . .

. Family 1 Cribrariidae

Genus **Cribraria** Persoon (Fig. 137, c)

Sporangia stalked; wall thickened and forms a delicate persistent network expanded at the nodes.

Sporangia solitary; stalked. Family 2 Liceidae

Genus **Orcadella** Wingate (Fig. 137, d)

Sporangia stalked, furnished with a lid of thinner substance.

Sporangium-wall membranous without granular deposits.

. Family 3 Tubulinidae

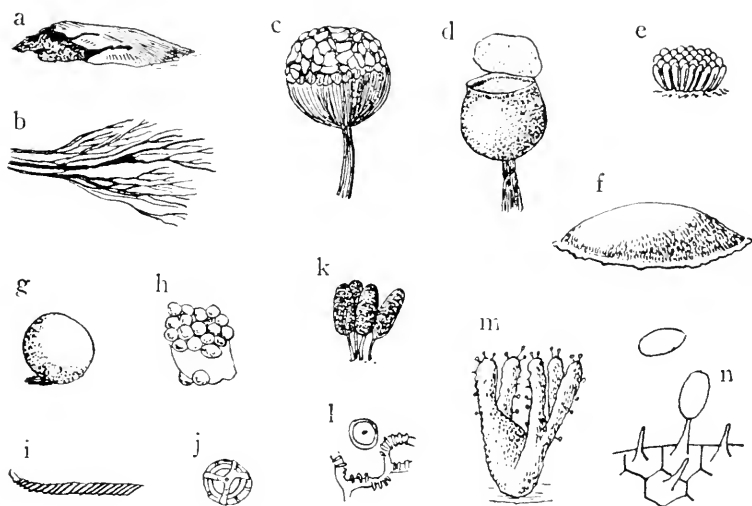


FIG. 137. a, b, *Amaurochaete fuliginosa* MacBride (a, group of sporangia, $\times \frac{1}{2}$; b, capillitium, $\times 10$) (Lister); c, Empty sporangium of *Cribraria aurantiaca* Schrader, $\times 20$ (Lister); d, sporangium of *Orcadella operculata* Wingate, $\times 80$ (Lister); e, Cluster of sporangia of *Tubulina fragiformis* Persoon, $\times 3$ (Lister); f, Aethalium of *Reticularia lycoperdon* Bull., $\times 1$ (Lister); g, Aethalium of *Lycogala miniatum* Persoon, $\times 1$ (Lister); h-j, *Trichia affinis* de Bary (h, group of sporangia, $\times 2$; i, elater, $\times 250$; j, spore, $\times 400$) (Lister); k, l, *Arcyria punicea* Persoon (k, four sporangia, $\times 2$; l, part of capillitium, $\times 250$ and a spore, $\times 560$) (Lister); m, n, *Ceratiomyxa fruticulosa* MacBride (m, sporophore, $\times 40$; n, part of mature sporophore, showing two spores, $\times 480$) (Lister).

Genus **Tubulina** Persoon (Fig. 137, e)

Sporangia without tubular extensions.

Many sporangia more or less closely fused to form large bodies (aethalia); sporangium-wall incomplete and perforated.
 Family 4 Reticulariidae

Genus **Reticularia** Bulliard (Fig. 137, f)

Walls of convoluted sporangia incomplete, forming tubes and folds with numerous anastomosing threads.

Sporangia forming aethalium. Family 5 Lycogalidae

Genus **Lycogala** Adanson (Fig. 137, *g*)

Capillitium a system of uniform threads. . Sublegion 2 Caloneminea
 Capillitium Threads with spiral or annular thickenings.
 Family 1 Trichiidae

Genus **Trichia** Haller (Fig. 137, *h-j*)

Capillitium abundant, consisting of free elasters with spiral thickenings.

Capillitium combined into an elastic network with thickenings in forms of cogs, half-rings, spines, or warts.
 Family 2 Arcyriidae

Genus **Arcyria** Wiggers (Fig. 137, *k, l*)

Sporangia stalked; sporangium-wall evanescent above, persistent and membranous in the lower third.

Capillitium abundant; sporangia normally sessile.
 Family 3 Margaritidae

Genus **Margarita** Lister

Capillitium profuse, long, coiled hair-like.

Spores develop on the surface of sporophores. . Tribe 2 Exosporeae
 Spores white; borne singly on filiform stalk.
 Family Ceratiomyxidae

Genus **Ceratiomyxa** Schröter (Fig. 137 *m, n*)Suborder 2 **Sorophora** Lister

Pseudoplasmodium incomplete; myxamoeba of limax-form.
 Family 1 Guttuliniidae
 Pseudoplasmodium complete; myxamoeba with short pointed pseudopodia. Family 2 Dictyosteliidae

The Proteomyxa and the Mycetozoa as outlined above, are not distinctly defined groups. In reality, there are a number of forms which stand on the border line between them.

Phytomyxinae Schröter

These organisms which possess a large multinucleate amoeboid body, are parasitic in various plants and also in a few animals. They do not form any sporangium and their methods of spore-formation are simple.

Genus **Plasmodiophora** Woronin. Parasitic in the root of the

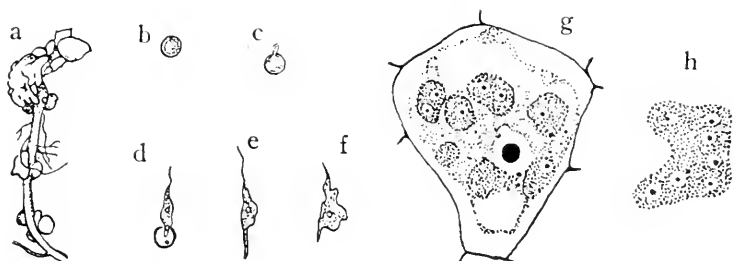


FIG. 138. *Plasmodiophora brassicae*. a, root-hernia of cabbage; b, a spore, $\times 620$; c-e, stages in germination of spore, $\times 620$; f, myxamoeba, $\times 620$ (Woronin); g, a host cell with several young parasites, $\times 400$; h, an older parasite, $\times 400$ (Nawaschin).

cabbage and other Cruciferae. The organism produces knotty enlargements, sometimes known as 'root-hernia,' or 'fingers and toes' (Fig. 138, a). The small spore (b) gives rise to a myxoflagellate (c-f) which penetrates into the host cell. The organism grows in size and the nucleus divides (g). Several myxamoebae fuse into a plasmodium, thus destroying the host cells. The nuclei undergo mitotic division and finally the plasmodium divides into a large number of simple spores.

P. brassicae W. (Fig. 138). In the species of *Brassica*.

Other genera are **Sorosphaera** Schröter, parasitic in *Veronica*; **Tetramyxa** Goebel, forming gall in *Ruppia*, etc.

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CHAPTER 18

Order 3 **Amoebina** Ehrenberg

THE Amoebina show a very little cortical differentiation. There is no pellicle or test, surrounding the body, although in some there are indications that a very thin and delicate pellicle exists. The cytoplasm is more or less distinctly differentiated into the ectoplasm and the endoplasm. The ectoplasm is hyaline and homogeneous, and appears tougher than the endoplasm. In the endoplasm which is granulated or vacuolated, are found one or more nuclei, various food vacuoles, crystals, and other inclusions. In the freshwater forms, there is at least one distinctly visible contractile vacuole. The pseudopodia are lobopodia, and ordinarily both the ectoplasm and endoplasm are found in them. They are formed by streaming or fountain movements of the cytoplasm. In some members of this order, the formation of pseudopodia is described as eruptive or explosive, since the granules present in the endoplasm break through the border line between the two cytoplasmic layers and suddenly flow into the pseudopodia.

The life-history is not completely known, even among the species of the genus *Amoeba*. Asexual reproduction is ordinarily by binary fission, although multiple fission may occasionally take place. Encystment is of common occurrence. Sexual reproduction, which has been reported in a few species, has not been confirmed.

The Amoebina inhabit all sorts of fresh, brackish and salt waters. They are also found in moist soil and on ground covered with decaying leaves. Many are inhabitants of the digestive tract of various animals, and some are pathogenic to the hosts.

The taxonomic status of the group is highly uncertain and confusing, since their life-histories are mostly unknown and since numerous protozoans other than the members of this group often possess amoeboid stages. Forms such as *Rhizomastigina* (p. 235) may be considered as belonging to either the Sarcodina or the Mastigophora.

The order is subdivided into three families as follows:

With amoeboid and flagellate stages.
Family 1 Dimastigamoebidae (p. 305)

Amoeboid stage only

With one or more nuclei of one kind

Free-living.....Family 2 Amoebidae (p. 306)

Parasitic.....Family 3 Endamoebidae (p. 312)

With a 'secondary nucleus'.....Family 4 Paramoebidae (p. 321)

Family 1 Dimastigamoebidae Wenyon

The members of the two genera placed in this family possess both amoeboid and flagellate phases (*diphasic*). In the former, the organism undergoes amoeboid movement by means of lobopodia and in the latter the body is more or less elongated. Binary fission seems to take place during the amoeboid phase only. Thus these are diphasic protozoans, in which the amoeboid stage predominates over the flagellate. The amoeboid phase resembles a 'limax' amoeba; under natural circumstances, it is often exceedingly difficult by observing the amoeboid stage only, to determine whether they belong to this family or the family Amoebidae.

Genus **Dimastigamoeba** Blochmann (*Naegleria* Alexeieff). Minute; flagellate stage with 2 flagella; amoeboid stage resembles Vahlkampfia (p. 310), with lobopodia; cytoplasm differentiated; vesicular nucleus with a large endosome; contractile vacuole conspicuous; food vacuoles contain bacteria; cysts uninucleate; free-living in stagnant water and often coprozoic.

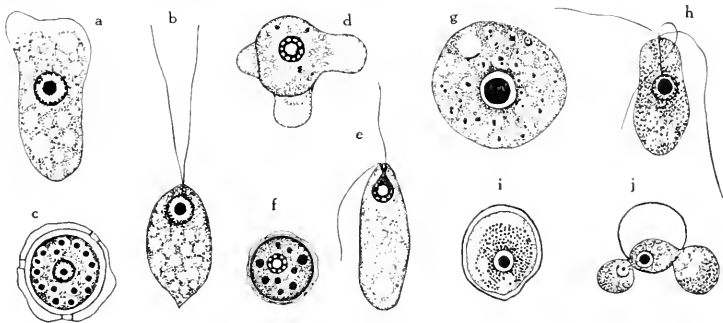


FIG. 139. a-c, trophozoite, flagellate phase and cyst (all stained) of *Dimastigamoeba gruberi*, $\times 750$ (Alexeieff); d-f, similar stages of *D. bistadialis*, $\times 750$ (Kühn); g-j, trophozoite, flagellate phase, cyst and excystation of *Trimastigamoeba philippinensis*, $\times 950$ (Whitmore).

D. gruberi (Schardinger) (Fig. 139, a-c). Amoeboid stage 10–50 μ long; cyst wall with several openings; flagellate stage 10–30 μ long.

D. bistadialis (Puschkarew) (Fig. 139, *d-f*). Similar in size; but cyst with a smooth wall.

Genus **Trimastigamoeba** Whitmore. Flagellate stage bears 3 flagella of nearly equal length; vesicular nucleus with a large endosome; amoeboid stage small, less than 20μ in diameter; uninucleate cysts with smooth wall; coprozoic. One species.

T. philippinensis W. (Fig. 139, *g-j*). Amoeboid stage $16-18\mu$ in diameter; oval cysts $13-14\mu$ by $8-12\mu$; flagellate stage $16-22\mu$ by $6-8\mu$.

Family 2 **Amoebidae** Bronn

These amoebae do not have flagellate stage and are exclusively amoeboid (*monophasic*). They are free-living in fresh or salt water, in damp soil, moss, etc., and a few parasitic; 1, 2, or many nuclei; contractile vacuoles in freshwater forms; multiplication by binary or multiple fission; encystment common.

Genus **Amoeba** Ehrenberg (*Chaos* Linnaeus; *Proteus* Müller; *Amiba* Bory). Amoeboid; naked, in a few species there are indications that a delicate pellicle occurs; usually with a nucleus, vesicular or somewhat compact; contractile vacuoles; pseudopodia mainly lobopodia, never anastomosing with one another; some students have used the nuclear structure for specific differentiation, but unfortunately not always clear; holozoic; fresh, brackish or salt water. Numerous species.

A. proteus (Pallas) (Figs. 25; 32, *b, c*; 39, *f*; 41-43; 140, *a, b*). Up to 600μ or longer in largest diameter; creeping with a few large lobopodia, showing longitudinal ridges; ectoplasm and endoplasm usually distinctly differentiated; typically uninucleate; nucleus discoidal, but polymorphic; endoplasmic crystals truncate bipyramid, up to 4.5μ long (Schaeffer); nuclear and cytosomic divisions show a distinct correlation (p. 137); fresh water.

A. discoides Schaeffer (Figs. 39, *g*; 140, *c*). About 400μ long during locomotion; a few blunt, smooth pseudopodia; crystals abundant, truncate bipyramidal, about 2.5μ long (Schaeffer); endoplasm with numerous coarse granules; fresh water.

A. dubia S. (Figs. 39, *h-l*; 140, *d*). About 400μ long; numerous pseudopodia flattened and with smooth surface; crystals, few, large, up to 30μ long and of various forms among which at least 4 types are said to be distinct; contractile vacuole one or more; fresh water.

A. verrucosa Ehrenberg (Figs. 32, *a, d-h*; 40, *a*; 140, *e*). Ovoid

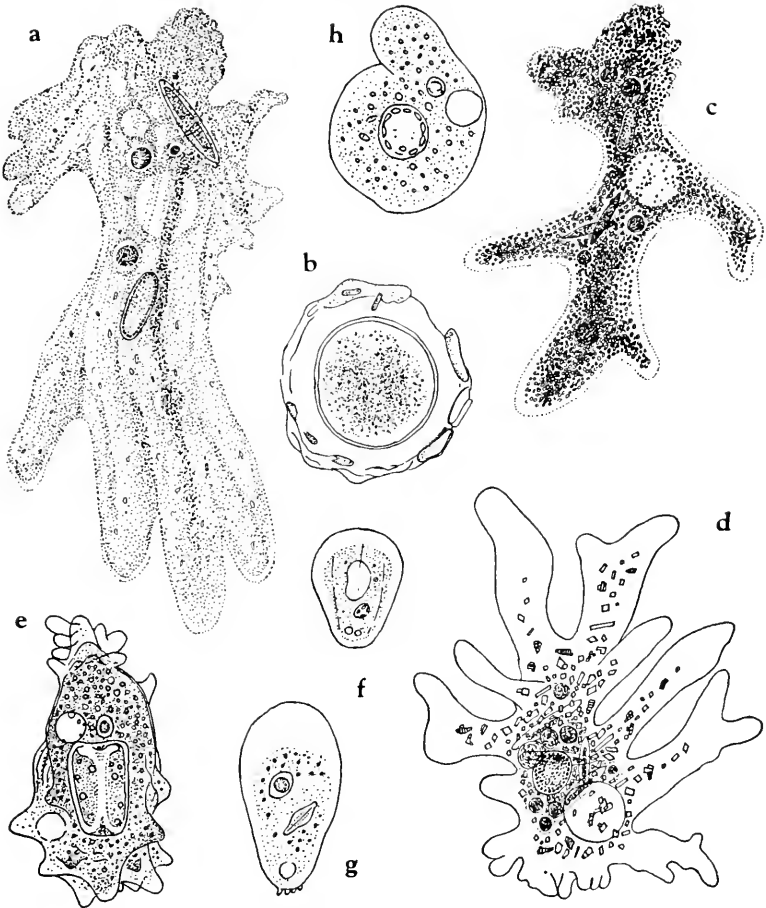


FIG. 140. a, b, *Amoeba proteus* (a, $\times 130$ (Schaeffer), b (Doflein)); c, *A. discoides*, $\times 130$ (Schaeffer); d, *A. dubia*, $\times 130$ (Schaeffer); e, *A. verrucosa*, $\times 200$ (Cash); f, *A. striata*, $\times 400$ (Penard); g, *A. guttula*, $\times 800$ (Penard); h, *A. limicola*, $\times 530$ (Penard).

in general outline with wart-like expansions; body surface usually wrinkled, with a definite pellicle; pseudopodia short, broad and blunt; nucleus ovoid; contractile vacuole; up to 200μ in diameter; fresh water among algae.

A. striata Penard (Fig. 140, f). Somewhat similar to *A. verrucosa*, but small; body flattened; ovoid, narrowed and rounded posteriorly; contractile vacuole comparatively large and often

not spherical; extremely delicate pellicle shows 3 or 4 fine longitudinal lines which appear and disappear with the movement of the body; $25\text{--}45\mu$ by $20\text{--}35\mu$; fresh water among vegetation.

A. guttula Dujardin (Fig. 140, *g*). Ovoid during locomotion, narrowed behind; often with a few minute, nipple-like dentations at the temporary posterior end; movement by wave-like expansions of ectoplasm; endoplasm granulated, with crystals; a single contractile vacuole; $30\text{--}35\mu$ by $20\text{--}25\mu$; fresh water in vegetation.

A. limicola Rumbler (Fig. 140, *h*). Somewhat similar to *A. guttula*; body more rounded; locomotion by eruption of cytoplasm through the body surface; $45\text{--}55\mu$ by 35μ ; fresh water among vegetation.

A. spumosa Gruber (Fig. 141, *a*). Somewhat fan-shaped; flattened; during locomotion broad pseudopodia with pointed end at temporary anterior region; posterior region with nipple-like projections; a small number of striae become visible during movement, showing there is a very thin pellicle; endoplasm always vacuolated, the vacuoles varying in size (up to 30μ in diameter); vesicular nucleus with an endosome; $50\text{--}125\mu$ long during locomotion; fresh water.

A. vespertilio Penard (Fig. 141, *b, c*). Pseudopodia conical, comparatively short, connected at base by web-like expansions of ectoplasm; endoplasm colorless, with numerous granules and food particles; a single nucleus with a large endosome; contractile vacuoles; $60\text{--}100\mu$ long; fresh water.

A. gorgonia P. (Fig. 141, *d-f*). Body globular when inactive with a variable number of radiating 'arms,' formed on all sides; locomotion by forming elongate pseudopodia, composed of both ectoplasm and endoplasm; $40\text{--}50\mu$ in diameter; extended forms about 100μ long; fresh water among vegetation.

A. radiosa Ehrenberg (Fig. 141, *g*). Small, usually inactive; globular or oval in outline; with 3–10 radiating slender pseudopodia which vary in length and degree of rigidity; when pseudopods are withdrawn, the organism may be similar to *A. proteus* in general appearance; pseudopods straight, curved or spirally coiled; size varies, usually about 30μ in diameter, up to 120μ or more; fresh water.

Genus **Dinamoeba** Leidy. Essentially Amoeba, but the temporary posterior region of body with retractile papillae; body surface including pseudopods and papillae, bristling with minute

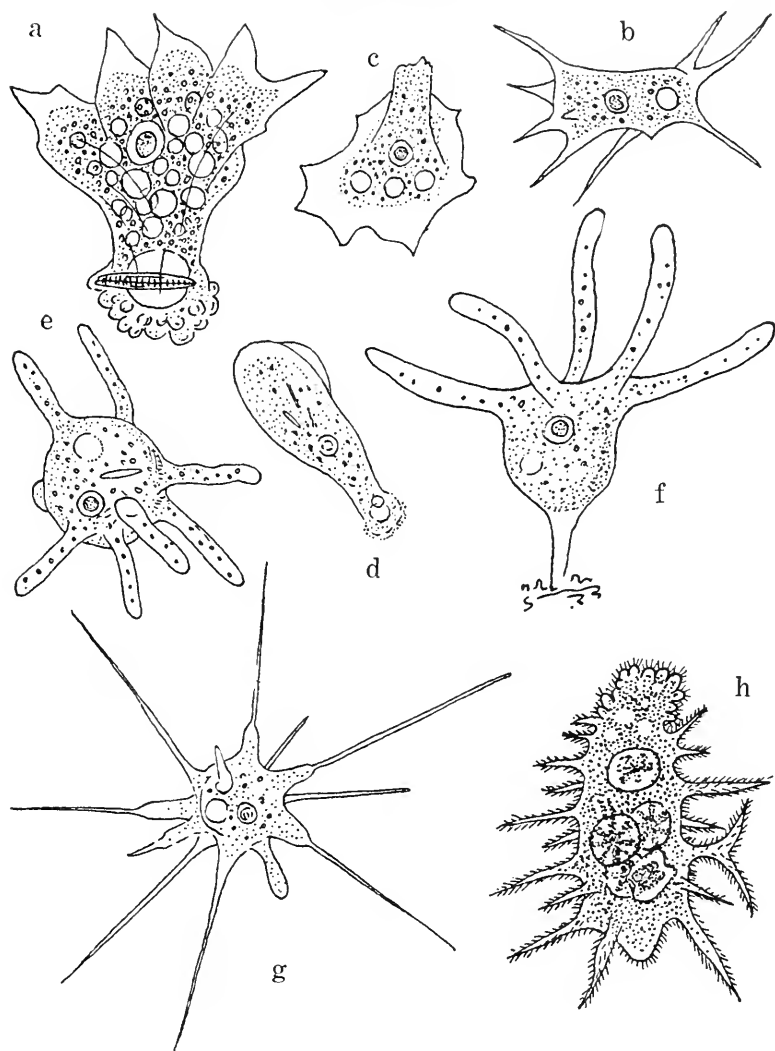


FIG. 141. a, *Amoeba spumosa*, $\times 400$ (Penard); b, c, *A. respertilio*, $\times 300$ (Penard); d-f, *A. gorgonia*, $\times 400$ (Penard); g, *A. radiosa*, $\times 500$ (Penard); h, *Dinamoeba mirabilis*, $\times 250$ (Leidy).

spicules or motionless cils; often surrounded by a thick layer of delicate hyaline jelly, even during locomotion; fresh water.

D. mirabilis L. (Fig. 141, h). Oval to limaciform; spheroid when

floating; pseudopodia numerous, conical; ectoplasm clear, usually with cils; endoplasm with food vacuoles, oil (?) spherules and large clear globules; nucleus and contractile vacuole obscure; spherical forms $64\text{--}160\mu$ in diameter; creeping forms $152\text{--}340\mu$ by $60\text{--}220\mu$; in sphagnum swamp.

Genus **Pelomyxa** Greeff. Large sluggish amoebae; with a few to numerous nuclei; cytoplasm poorly differentiated; pseudopodia few, short, and broad; animal undergoes rolling movement; with diatoms, bacteria, water vacuoles, sand grains and refractile bodies which are thought to be either reserve food material similar to glycogen or metabolic products used by symbiotic bacteria; contractile vacuole has not been noticed with certainty, multiplication by binary fission; gamete formation has been reported; it is presumed that uninucleate bodies undergo fusion to form zygotes which develop into multinucleate forms; fresh water. Several species.

P. palustris G. (Fig. 142, a). Large; $150\mu\text{--}2\text{ mm.}$ or larger in diameter; sluggish with one broad pseudopodium by which the organism undergoes rolling movement; cytoplasm undifferentiated; numerous vacuoles and nuclei; various inclusions often color the body brown to black and make it appear opaque; symbiotic protophytan, *Cladophrix pelomyxae* Velez, occurs regularly; cysts with 2-3 envelopes; cyst contents divide into several multinucleate bodies; in stagnant water, creeping on the muddy bottom.

P. villosa (Leidy) (Fig. 142, b). Similar to the last-named species, but somewhat smaller; with numerous short and papillary villi at posterior extremity; during locomotion, about 250μ long; in the ooze of freshwater bodies.

Genus **Vahlkampfia** Chatton et Lalung-Bonnaire. Small amoebae; vesicular nucleus with a large endosome and peripheral chromatin; with polar caps during nuclear division; snail-like movement, with one broad pseudopodium; cysts with a perforated wall; fresh water or parasitic.

V. limax (Dujardin) (Fig. 142, c). $30\text{--}40\mu$ long; fresh water.

V. patuxent Hogue (Fig. 142, d). In the alimentary canal of the oyster; about 20μ long during the first few days of artificial cultivation, but later reaching as long as 140μ in diameter; ordinarily one large broad fan-shaped pseudopodium composed of the ectoplasm; in culture, pseudopodium-formation eruptive; holozoic on

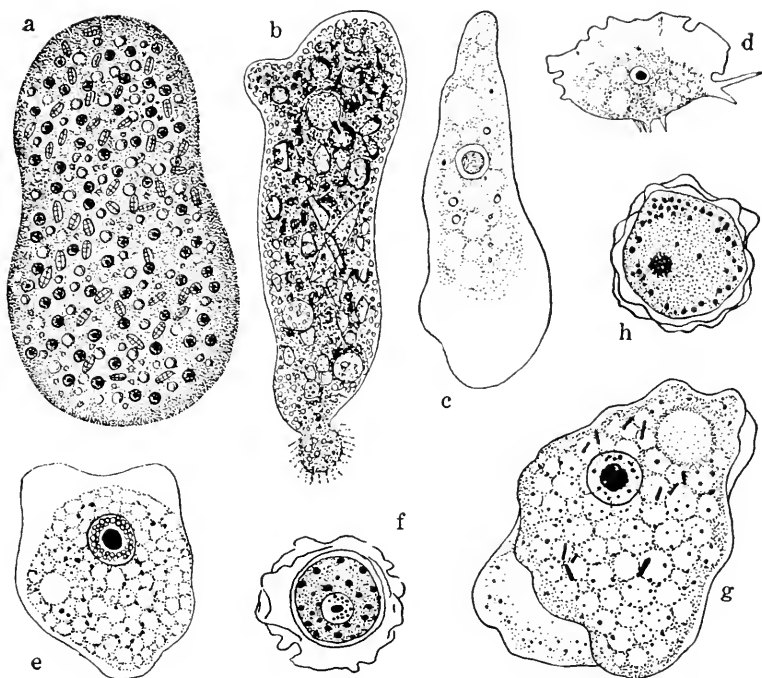


FIG. 142. a, *Pelomyxa palustris*, $\times 130$ (Kühn); b, *P. villosa*, $\times 420$ (Leidy); c, *Vahlkampfia limax*, $\times 830$ (Kudo); d, *V. patuxent*, $\times 830$ (Hogue); e, f, *Hartmannella hyalina*, $\times 1170$ (Dobell); g, h, *H. castellanii*, $\times 1590$ (Hewitt).

bacteria; multiplication by fission or budding; encystment rare; cysts uninucleate.

Genus **Hartmannella** Alexeieff. Small amoebae with the following nuclear characteristics: vesicular; large endosome central and chromatin granules scattered along the periphery; at the time of division endosome disintegrates and chromosomes and spindle fibers appear; there are no so-called polar caps during division as are found in *Vahlkampfia*, from which differentiation is difficult.

H. hyalina (Dangeard) (Fig. 142, e, f). Body more or less rounded; less than 20μ in diameter; a contractile vacuole; binary fission; spherical cyst, $10\text{--}15\mu$ in diameter, covered with a smooth inner and a much wrinkled outer wall; easily cultivated from old faeces of man and animals; also in soil and fresh water.

H. castellanii Douglas (Fig. 142, g, h). In association with fungi

and certain bacteria; Hewitt obtained it from agar cultures of a sample soil taken from among the roots of white clover; co-existing with yeast-like fungi, *Flavobacterium trifolium* and *Rhizobium* sp.; 12–30 μ in diameter; cyst membrane without pore; some cysts viable at 37°C. for 6 days.

Genus **Sappinia** Dangeard. With two closely associated nuclei.

S. diploidea (Hartmann et Nögler). Coprozoic in the faeces of different animals; pseudopodia short, broad, and few; highly vacuolated endoplasm with 2 nuclei, food vacuoles, and a contractile vacuole; surface sometimes wrinkled; the nuclei divide simultaneously; during encystment, two individuals come together and secrete a common cyst wall; 2 nuclei fuse so that each individual possesses a single nucleus; finally cytoplasmic masses unite into one; each nucleus gives off reduction bodies (?) which degenerate; 2 nuclei now come in contact without fusion, thus producing a binucleate cyst (Hartmann and Nögler).

Family 3 **Endamoebidae** Calkins

Exclusively endoparasitic amoebae; the vegetative form is relatively small and occurs mostly in the alimentary canal of the host; contractile vacuoles absent, except in *Hydramoeba*; multiplication by binary fission; encystment common. The generic differentiation is based upon morphological characteristics of the nucleus. Summary No. 99 of 'Opinions Rendered' by the International Commission of Zoological Nomenclature (1928) holds that *Entamoeba* is a synonym of *Endamoeba*; in the present work, however, *Endamoeba* and *Entamoeba* are separated, since the two groups of species placed under them possess different nuclear characteristics and since it is not advisable to establish another generic name in place of *Entamoeba* which has been so frequently and widely used throughout the world.

Genus **Endamoeba** Leidy. Nucleus spheroidal to ovoid; membrane thick; in life, filled with numerous granules of uniform dimensions along its peripheral region; upon fixation, a fine chromatic network becomes noticeable in their stead; central portion coarsely reticulated; with several endosomes between the two zones; in some, cytoplasm becomes prominently striated during locomotion; in the intestine of invertebrates.

E. blattae (Bütschli) (Figs. 49; 143). In the colon of cockroaches; 10–150 μ in diameter; rounded individuals with broad

pseudopodia, show a distinct differentiation of cytoplasm; elongated forms with a few pseudopodia, show ectoplasm only at the extremities of the pseudopods; endoplasm of actively motile trophozoites shows a distinct striation, a condition not often seen in other amoebae; fluid-filled vacuoles occur in large numbers; amoebae feed on starch grains, yeast cells, bacteria and protozoans, all of which coexist in the host organ; cysts commonly

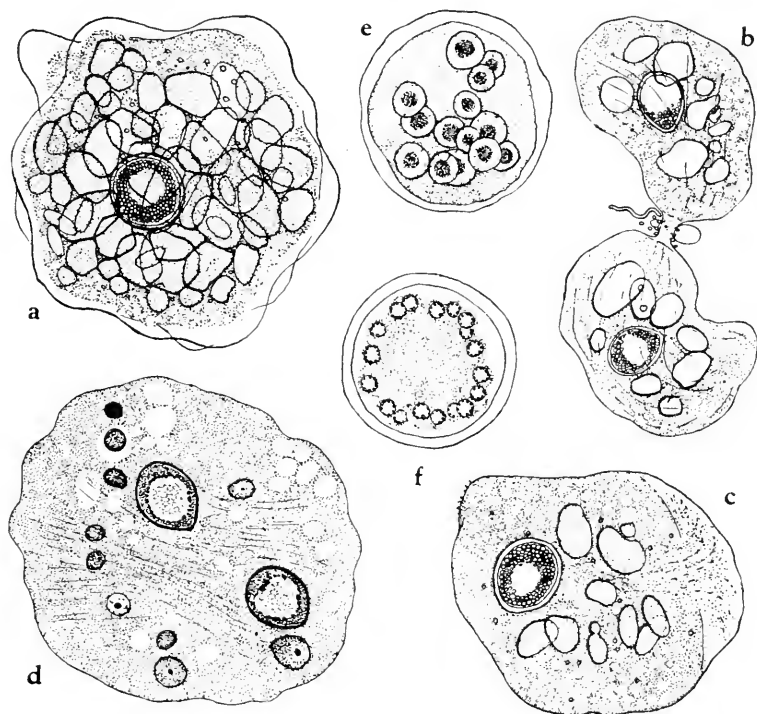


FIG. 143. *Endamoeba blattae*. a-c, $\times 530$; d-f, $\times 700$ (Kudo).

seen in the colon contents, with often more than 60 nuclei. The life-cycle of this amoeba is still unknown. Mercier (1909) held that when the multinucleate cysts gain entrance to the host intestine through its mouth, each of the cyst-nuclei becomes the center of a gamete; when the cyst-membrane ruptures, the gametes are set free and anisogamy takes place, resulting in formation of numerous zygotes which develop into the habitual trophozoites. Among the more recent investigators, Morris (1936) is

inclined to think that sexual reproduction brings about 'zygotic adults.' The nucleus has been studied by Meglitsch (1939).

E. thomsoni Lucas. In colon of the cockroaches; 7–30 μ in diameter; very adhesive; 1–3 chromatin blocks on the nuclear membrane; cysts 8–16 μ in diameter, with 1–4 nuclei.

E. disparata Kirby. In colon of *Microtermes hispaniolae*; 20–40 μ long; active; xylophilous.

E. majestas K. (Fig. 144, a). In the same habitat; 65–165 μ in diameter; many short pseudopodia; cytoplasm filled with food particles.

E. simulans K. (Fig. 144, b). In the gut of *Microtermes panamaensis*; 50–150 μ in diameter.

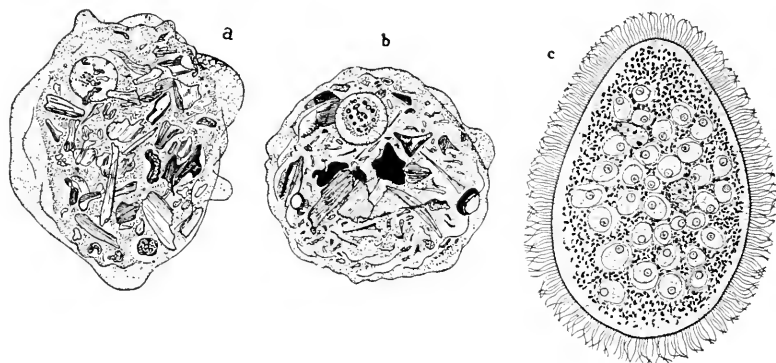


FIG. 144. a, *Endamoeba majestas*, $\times 420$ (Kirby); b, *E. simulans*, $\times 420$ (Kirby); c, *Entamoeba brasiliensis* in *Zelleriella*, $\times 290$ (Stabler and Chen).

E. sabulosa K. In the same habitat; small, 19–35 μ in diameter

Genus **Entamoeba** Casagrandi et Barbagallo. Nucleus vesicular, with a comparatively small endosome, located in or near the center and with varying number of peripheral chromatin granules attached to the nuclear membrane. It was established by the two Italian authors who were unaware of the existence of the genus *Endamoeba* (p. 312). Numerous species in vertebrates or invertebrates.

E. histolytica Schaudinn (Fig. 145, a–f). 20–30 μ in diameter; cytoplasm usually differentiated distinctly; eruptive formation of large lobopodia, composed exclusively of ectoplasm; the vesicular nucleus appears in life as a ring, difficult to recognize; food vacu-

oles contain erythrocytes, tissue cells, leucocytes, etc.; stained nucleus shows a membrane, peripheral chromatin granules, a centrally located small endosome, and indistinct network with a few scattered chromatin granules. The trophozoites invade the tissues of the gut-wall of man and multiply by binary fission. Under certain circumstances not well understood, the amoeba extrudes its food material and becomes smaller in size, possibly by division also. Such a form is sluggish and shows frequently glycogen bodies and elongated refractile bodies which stain deeply with a nuclear stain (hence called chromatoid bodies). This stage is known as the precystic stage. The cyst is formed when the precystic form ceases to move about and becomes surrounded by a definite cyst-membrane which it secretes. The cysts measure 5–20 μ in diameter. At first it contains a single nucleus which divides twice and tetranucleate cyst is thus formed. The glycogen and chromatoid bodies become absorbed, as the cyst grows older. The change between the cyst and the young trophozoite is not definitely known, although in recent years several investigators such as Dobell, Cleveland and Sanders and others, have been able to cultivate the amoeba *in vitro* and noted the excystment followed by division into up to 8 uninucleate amoebulae, each of which grows into a mature trophozoite. There is no evidence that sexual reproduction occurs in its development.

This amoeba was first definitely recognized by Lösch in Russia in 1875. It is now known to have a wide geographical distribution. The incidence of infection in man depends mainly upon the sanitary conditions of the community, since the amoeba is carried from man to man in the encysted stage. Faecal examinations which have been carried on by numerous investigators in different parts of the world, reveal that the incidence of the infection runs as high as 50 per cent. In the United States 49,336 examinations conducted in various localities show infection rate varied from 0.2–53 per cent, averaging 11.6 per cent, which justifies Craig's (1926) early estimate that ten per cent of the general population harbor this organism. An acute infection by *Entamoeba histolytica* is accompanied by dysentery, while in chronic cases, the host may void a number of infective cysts without suffering himself. Such a person is known as a 'carrier.' The amoeba invades the liver also and produces in it various abscesses of a serious nature. Numerous varieties are known. Cats and dogs are easily infected

especially *per anum* by this amoeba and show typical symptoms. Spontaneous dysentery among cats due to this organism has also been noticed.

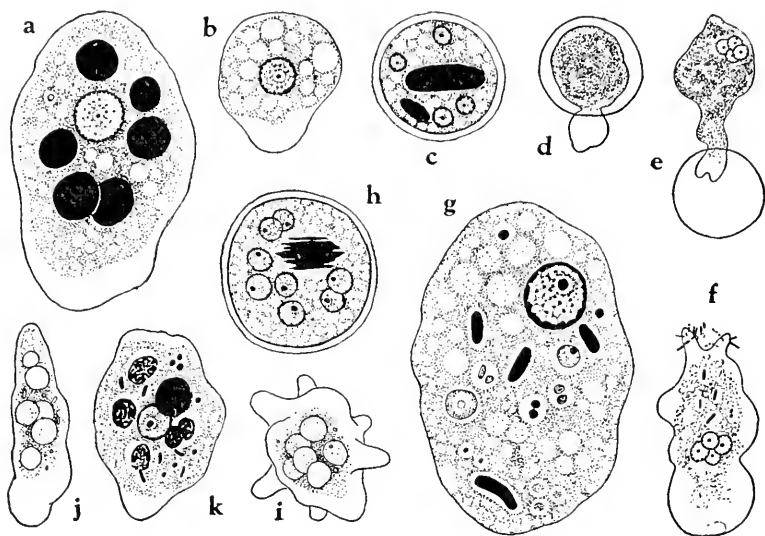


FIG. 145. a-f, *Entamoeba histolytica* (a, trophozoite; b, precystic stage; c, cyst, $\times 1330$; d-f, excystment, $\times 930$) (a-c (Kudo); d-f (Yorke and Adams)); g, h, *E. coli*, $\times 1330$ (Kudo); i-k, *E. gingivalis*, $\times 670$ (Kudo).

E. coli (Lösch) (Fig. 145, g, h). Trophozoites $15-40\mu$ in diameter; cytoplasm indistinctly differentiated; lobopodia slowly formed and movement sluggish; food vacuoles contain varying number of bacteria, also erythrocytes in a few cases (Tyzzer and Geiman); nucleus observable *in vivo*; compared with *E. histolytica*, the endosome is somewhat larger and located eccentrically and peripheral chromatin granules more conspicuous; multiplication by binary fission; precystic stage very similar in appearance to that of *E. histolytica*; mature cyst contains normally 8 nuclei and measures $10-30\mu$ in diameter; in young cysts there are glycogen bodies which are comparatively larger than those found in the last-named species; chromatoid bodies splinter-like and often grouped. This amoeba seems to have been observed first by Lewis in 1870 in India. It is a commensal in the human intestine and widely distributed throughout the world.

E. gingivalis (Gros) (*E. buccalis* Prowazek) (Fig. 145, *i-k*). Fairly active amoeba; a few lobopodia are formed and retracted rapidly; 10–40 μ long, the majority measuring 10–20 μ in diameter; cytoplasm distinctly differentiated; endoplasm with host tissue cells, bacteria, etc.; nucleus similar to that of *E. histolytica*, but endosome not always central; multiplication by binary fission; cyst is unknown, and therefore transmission of the amoeba from man to man is considered to be direct.

This amoeba is the first endoparasitic amoeba known to man and was observed by Gros in 1849 in human tartar. As to the effect of the amoeba upon the host, some workers believe that it is the probable cause of pyorrhoea alveolaris, while the majority of investigators are inclined to think that it is a commensal of the human mouth.

E. gedoelsti Hsiung (*E. intestinalis* (Gedoelst)). In colon and caecum of horse; 6–13 μ by 6–11 μ ; endosome eccentric; bacteria-feeder.

E. equi Fantham. 40–50 μ by 23–29 μ ; nucleus oval; cysts tetranucleate, 15–24 μ in diameter; seen in the faeces of horse; Fantham reports that the endoplasm contained erythrocytes.

E. bovis Liebetanz. 5–20 μ in diameter; in stomach of cattle.

E. ovis Swellengrebel. Cyst uninucleate; in intestine of sheep.

E. caprae Fantham. In goat intestine.

E. polecki (Prowazek). In colon of pigs; 10–12 μ in diameter; cyst uninucleate.

E. debliccki Nieschulz. In intestine of pig; 5–10 μ in diameter; cyst uninucleate.

E. venaticum Darling. In colon of dog; similar to *E. histolytica*; since the dog is experimentally infected with the latter, this amoeba discovered from spontaneous amoebic dysentery cases of dogs, in one of which was noted abscesses of liver, is probably *E. histolytica*.

E. cuniculi Brug. Similar to *E. coli* in both trophic and encysted stages; in intestine of rabbits.

E. cobayae Walker (*E. caviae* Chatton). Similar to *E. coli*; in intestine of guinea-pigs.

E. muris (Grassi). Similar to *E. coli*; in intestine of rats and mice.

E. gallinarum Tyzzer. In fowls intestine; cysts octonucleate.

E. testudinis Hartmann. In intestine of turtles, *Testudo graeca*, *T. argentina*, *T. calcarata* and *Terrapene carolina*.

E. barreti Taliaferro et Holmes. In colon of snapping turtle, *Chelydra serpentina*.

E. terrapinae Sanders et Cleveland. Trophozoites 10–15 μ long; cysts 8–14 μ in diameter, tetranucleate when mature; in colon of *Chrysemys elegans*.

E. serpentis da Cunha et da Fonseca. In intestine of the snake, *Drimobius bifossatus* in South America.

E. ranarum (Grassi) (Fig. 146, *a, b*). In colon of various species of frogs; resembles *E. histolytica*; 10–50 μ in diameter; cysts are usually tetranucleate, but some contain as many as 16 nuclei; amoebic abscess of the liver was reported in one frog.

E. minchini Mackinnon. In gut of tipulid larvae; 5–30 μ in diameter; cyst nuclei up to 10 in number.

E. mesnili Keilin. In gut of dipterous insects, *Trichocera hiemalis* and *T. annulata* (larvae); 6–24 μ long and multinucleate; plasmotomy; cysts 8–11 μ in diameter, with 2 or 4 nuclei.

E. apis Fantham et Porter. In *Apis mellifica*; similar to *E. coli*.

E. brasiliensis (Carini) (Fig. 144, *c*). In the cytoplasm of many species of Protociliata; trophozoites 5.3–14.3 μ in diameter; cysts about 9.4 μ in diameter, uninucleate; no effect upon host ciliates even in case of heavy infection (Stabler and Chen).

Genus **Endolimax** Kuenen et Swellengrebel. Small; vesicular nucleus with a comparatively large irregularly shaped endosome, composed of chromatin granules embedded in an achromatic ground mass and several achromatic threads seen connecting the endosome with membrane; commensal in hindgut in man or animals. Several species.

E. nana (Wenyon et O'Connor) (Fig. 146, *c, d*). In colon of man; lobopodia formed quite actively, but sluggish; 6–12 μ in diameter; cytoplasm fairly well differentiated into 2 zones; nucleus difficult to make out in life; food vacuoles contain bacteria; cyst ovoid, 8–10 μ in diameter, tetranucleate when mature; widely distributed.

E. gregariniformis (Tyzzer). In caecum of fowls; 4–12 μ in diameter; cysts uninucleate.

E. ranarum Epstein et Ilovaisky (Fig. 146, *e, f*). In colon of frogs; cyst octonucleate, up to 25 μ in diameter.

E. blattae Lucas. In colon of cockroaches; 3–15 μ long; cyst with more than one nucleus.

Genus **Iodamoeba** Dobell. Vesicular nucleus, with a large en-

dosome rich in chromatin, a layer of globules which surrounds the endosome and which do not stain deeply, and achromatic strands between the endosome and membrane; cysts ordinarily uninucleate, contain a large glycogenous vacuole which stains conspicuously with iodine; in intestine of man or mammals.

I. butschlii (Prowazek) (*I. williamsi* (P.)) (Fig. 146, g, h). In colon of man; sluggish; 9–18 μ in diameter; cytoplasm with bacteria in food vacuoles; cysts mostly irregular in shape, 6–15 μ in diameter.

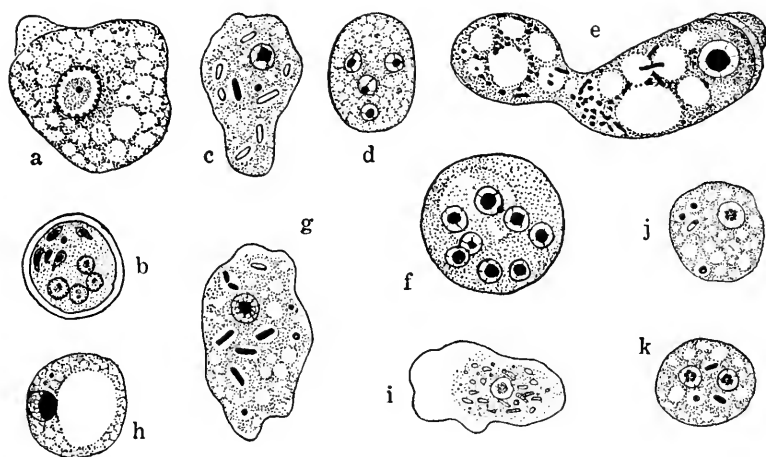


FIG. 146. a, b, *Entamoeba ranarum*, $\times 1090$ (Mercier and Mathis); c, d, *Endolimax nana*, $\times 1670$ (Kudo); e, f, *E. ranarum*, $\times 840$ (Epstein and Ilovaisky); g, h, *Iodamoeba bütschlii*, $\times 1670$ (Kudo); i–k, *Dientamoeba fragilis*, $\times 1840$ (Kudo).

I. suis O'Connor. In colon of pig; widely distributed; indistinguishable from *I. butschlii*; it is considered by some that pigs are probably reservoir host of *I. butschlii*.

Genus **Dientamoeba** Jepps et Dobell. Small amoeba; number of binucleate trophozoites often greater than that of uninucleate forms; nuclear membrane delicate; endosome consists of several chromatin granules embedded in plasmosomic substances and connected with the membrane by delicate strands; in colon of man.

D. fragilis J. et D. (Fig. 146, i–k). 4–12 μ long; cysts unknown.

Genus **Schizamoeba** Davis. Nucleus vesicular, without endo-

some, but with chromatin granules arranged along nuclear membrane; 1 to many nuclei; cyst-nuclei formed by fragmentation of those of the trophozoite and possess a large rounded chromatic endosome, connected at one side with the nuclear membrane by achromatic strands, to which chromatin granules are attached; in stomach of salmonoid fish. One species.

S. salmonis D. (Fig. 147, *a*, *b*). Sluggish amoeba; 10–25 μ in diameter; 1 to several nuclei; multiplication by binary fission; nuclear division amitotic. Cysts are said to be more abundant than trophozoites and their appearance seems to be correlated with the amount of available food; cysts spherical, 15–35 μ in diameter;

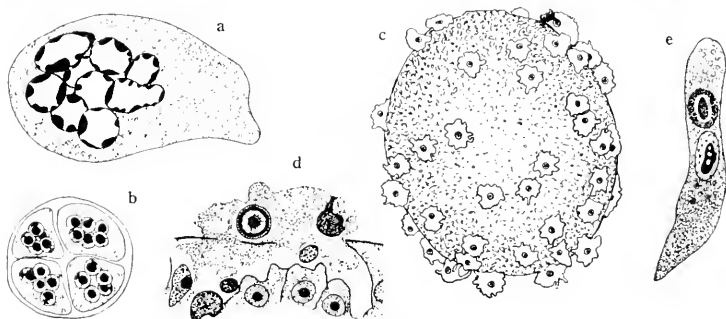


FIG. 147. *a*, *b*, *Schizamoeba salmonis*, $\times 800$ (Davis); *c*, *d*, *Hydraamoeba hydroxena* (*c*, a heavily infected *Hydra oligactis* which lost its tentacles, $\times 70$; *d*, section of an infected hydra showing a trophozoite feeding on ectodermal cells, $\times 350$) (Reynolds and Looper); *e*, *Paramoeba pigmentifera* with its nucleus in the center, $\times 600$ (Janicki).

cyst-membrane thin and nuclei vary from 3 to many; during encystment, chromatin bodies of trophozoite become collected in several masses which then disintegrate and each chromatin grain becomes the endosome of newly formed nucleus; cyst contents divide sooner or later into 4–11 multinucleate bodies and the whole increases in size; finally cyst-membrane disintegrates and the multinucleate bodies become set free. Trophozoites are said to occur in the mucous covering of stomach of host fish; cysts occur in both stomach and intestine. Aside from the loss of certain amount of available food, no pathogenic effect of the amoeba upon the host fish was noticed by Davis.

Genus **Hydramoeba** Reynolds et Looper. Nucleus vesicular with a large central endosome composed of a centriole (?) and chromatin granules embedded in an achromatic mass, achromatic

strands radiating from endosome to membrane; a ring made up of numerous rod-shaped chromatin bodies in the nuclear-sap zone; 1 or more contractile vacuoles; apparently the most primitive parasitic amoeba; parasitic on Hydra.

H. hydroxena (Entz) (Fig. 147, *c, d*). Parasitic in various species of Hydra; first observed by Entz; Wermel found 90 per cent of Hydra he studied in Russia were infected by the amoeba; Reynolds and Looper stated that infected Hydra die on an average in 6.8 days and that the amoebae disappear in 4–10 days if removed from a host Hydra. More or less spheroidal, with blunt pseudopods; 60–380 μ in diameter; nucleus shows some 20 refractile peripheral granules in life; contractile vacuoles; food vacuoles contain host cells; multiplication by binary fission; encystment has not been observed.

Family 4 **Paramoebidae** Poche

Genus **Paramoeba** Schaudinn. The amoeba possesses a nucleus and nucleus-like secondary cytoplasmic structure, both of which multiply by division simultaneously; free-living or parasitic.

P. pigmentifera (Grassi) (Fig. 147, *e*). About 30 μ long; sluggish; cytoplasm distinctly differentiated; secondary body larger than the nucleus; flagellated swimmers are said to occur; parasitic in coelom of Chaetognatha such as *Sagitta claparedi*, *Spadella bipunctata*, *S. inflata*, and *S. serratodentata*.

P. schaudinni Faria, da Cunha et Pinto. About 7–22 μ in diameter; in salt water; Rio de Janeiro, Brazil.

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CHAPTER 19

Order 4 **Testacea** Schultze

THE Testacea or Thecamoeba comprise those amoeboid organisms which are enveloped by a simple shell or test, within which the body can completely be withdrawn. The shell has usually a single aperture through which pseudopodia protrude, and varies in shape and structure, although a chitinous or pseudo-chitinous membrane forms the basis of all. It may be thickened, as in *Arcella* and others, or composed of foreign bodies cemented together as in *Diffugia*, while in *Euglypha* siliceous platelets or scales are formed in the endoplasm and deposited on the membrane.

The cytoplasm is ordinarily differentiated into the ectoplasm and endoplasm. The ectoplasm is conspicuously observable at the aperture of the shell where filopodia or slender ectoplasmic lobopodia are produced. The endoplasm is granulated or vacuolated and contains food vacuoles, contractile vacuoles and nuclei. In some forms there are present regularly in the cytoplasm numerous basophilic granules which are known as 'chromidia' (p. 35).

Asexual reproduction is either by longitudinal fission in the forms with soft tests, or by transverse division or budding, while in others multiple division occurs. Encystment is common. Sexual reproduction by amoeboid or flagellate gametes has been reported in some species.

The testaceans are mostly inhabitants of fresh water, but some live in salt water and others are semi-terrestrial, being found in moss or moist soil, especially peaty soil.

Shell simple and membranous

Filopodia, often anastomosing..... Family 1 Gromiidae

Pseudopodia filose, simply branched... Family 2 Arcellidae (p. 327)

Shell with foreign bodies, platelets, or scales

With foreign bodies..... Family 3 Diffugiidae (p. 334).

With platelets or scales..... Family 4 Euglyphidae (p. 339).

Family 1 **Gromiidae** Eimer et Fickert

These forms are frequently included in the Foraminifera by other authors.

Genus **Gromia** Dujardin (*Allogromia*, *Rhynchogromia*, *Diplo-*

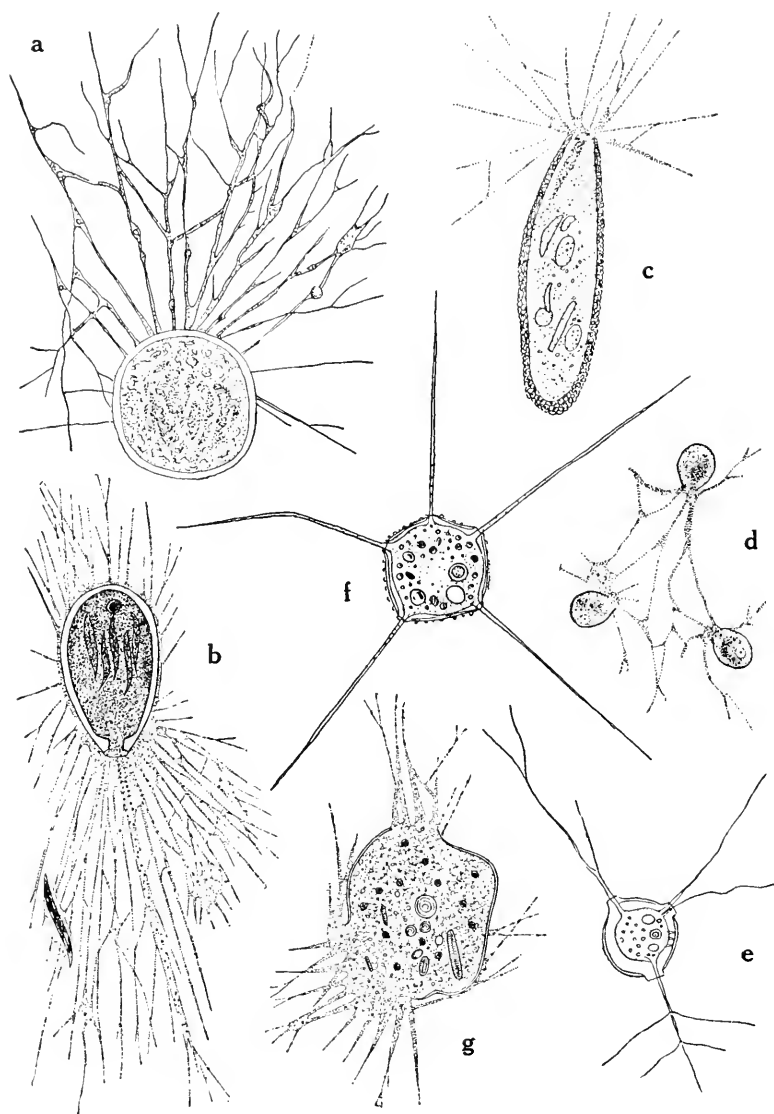


FIG. 148. a, *Gromia fluvialis*, $\times 120$ (Dujardin); b, *G. ovoidea*, $\times 50$ (Schultze); c, *G. nigricans*, $\times 200$ (Cash and Wailes); d, *Microgromia socialis*, $\times 170$ (Cash); e, *Microcometes paludosa*, $\times 670?$ (Penard); f, *Artodiscus saltans*, $\times 670$ (Penard); g, *Schultzeella difflucens*, $\times 120$ (Rhumbler).

gromia, Rhumbler). Thin test rigid or flexible, smooth or slightly coated with foreign bodies; spherical to elongate ellipsoid; aperture terminal; 1 or more nuclei; contractile vacuoles; many filopodia, branching and anastomosing; cytoplasm with numerous motile granules; fresh or salt water. Many species.

G. fluvialis D. (Fig. 148, *a*). Test spherical to subspherical; smooth or sparsely covered with siliceous particles; yellowish cytoplasm fills the test; aperture not seen; a large nucleus and numerous contractile vacuoles; filopodia long, often enveloping test; 90–250 μ long; on aquatic plants, in moss or soil.

G. ovoidea (Rhumbler) (Fig. 148, *b*). In salt water.

G. nigricans (Penard) (Fig. 148, *c*). Test large, circular in cross-section; a single nucleus; 220–400 μ long; in pond water among vegetation.

Genus **Microgromia** Hertwig et Lesser. Test small, hyaline, spherical or pyriform, not compressed; aperture terminal, circular; filopodia long straight or anastomosing, arising from a peduncle; a single nucleus and contractile vacuole; solitary or grouped.

M. socialis (Archer) (Fig. 148, *d*). Cytoplasm bluish; contractile vacuole near aperture; filopodia arise from a peduncle, attenuate, branching, anastomosing; often numerous individuals are grouped; multiplication by fission and also by swarmers; 25–35 μ in diameter; among vegetation in fresh water.

Genus **Microcometes** Cienkowski. Body globular, enclosed within a transparent, delicate, light yellowish and pliable envelope with 3–5 apertures, through which long branching filopodia extend; body protoplasm occupies about 1/2 the space of envelope; 1–2 contractile vacuoles; fresh water.

M. paludosa C. (Fig. 148, *e*). About 16–17 μ in diameter; fresh water among algae.

Genus **Artodiscus** Penard. Body globular, plastic; covered by envelope containing small grains of various kinds; nucleus eccentric; a few pseudopodia extend through pores of the envelope; movement very rapid; fresh water.

A. saltans P. (Fig. 148, *f*). 18–23 μ in diameter; fresh water.

Genus **Lieberkuhnia** Claparède et Lachmann. Test ovoidal or spherical, with or without attached foreign particles; aperture usually single, lateral or subterminal; one or more nuclei; many contractile vacuoles; pseudopodia formed from a long peduncle, reticulate, often enveloping test; fresh or salt water.

L. wagneri C. et L. (Fig. 149, a). Spheroidal; aperture subterminal, oblique, flexible; cytoplasm slightly yellowish, fills the test; 80–150 vesicular nuclei; many contractile vacuoles; pseudopodia long, anastomosing; 60–160 μ long; nuclei 6 μ in diameter; among algae in fresh and salt water.

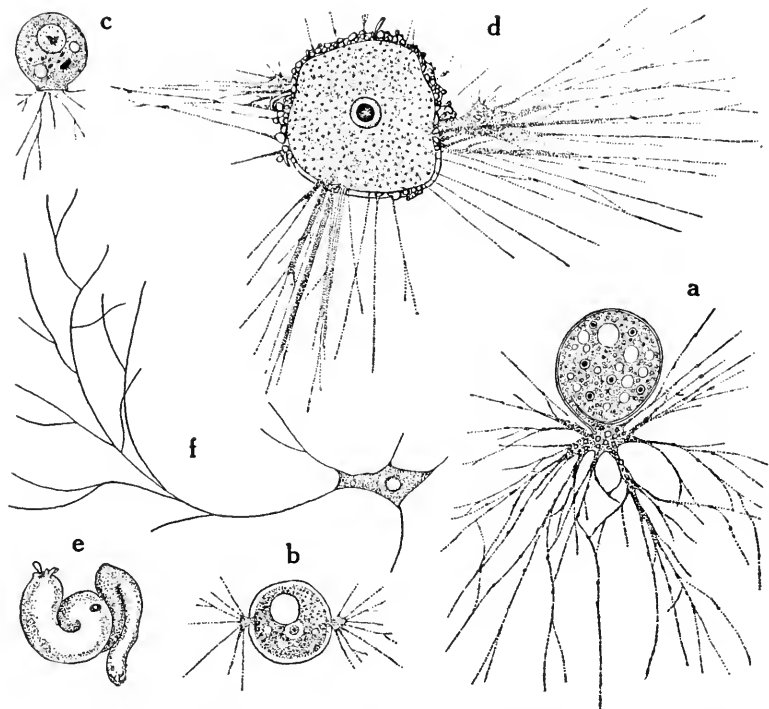


FIG. 149. a, *Lieberkuhiuia wagneri*, $\times 160$ (Verworn); b, *Diplophrys archeri*, $\times 930$ (Hertwig and Lesser); c, *Lecythium hyalinum*, $\times 330$ (Cash and Wailes); d, *Myxotheca arenilega*, $\times 70$ (Schaudinn); e, *Dactylosaccus vermiformis*, $\times 15$ (Rhumbler); f, *Boderia turneri* (Wright).

Genus **Diplophrys** Barker. Test thin, spherical; 2 apertures, one at each pole; cytoplasm colorless; a single nucleus; several contractile vacuoles; filopodia radiating. One species.

D. archeri B. (Fig. 149, b). With 1–3 colored oil droplets; pseudopodia highly attenuate, radiating, straight or branched; multiplication into 2 or 4 daughter individuals; solitary or in groups; diameter 8–20 μ ; on submerged plants in fresh water.

Genus **Lecythium** Hertwig et Lesser. Test thin, flexible, color-

less; aperture elastic, terminal; colorless cytoplasm fills the test; large nucleus posterior; numerous filopodia long, branching, not anastomosing; fresh water.

L. hyalinum (Ehrenberg) (Fig. 149, c). Spheroidal; aperture circular with a short flexible neck; a single contractile vacuole; diameter 20–45 μ ; in submerged vegetation.

Genus **Schultzeella** Rhumbler. Test thin, delicate, difficult to recognize in life, easily broken at any point for formation of pseudopodia which branch and anastomose; irregularly rounded; without foreign material; salt water.

S. diffluens (Grubler) (Fig. 148, g). Cytoplasm finely granulated; opaque colorless; with oil droplets, vacuoles and numerous small nuclei; up to 220 μ in diameter.

Genus **Myxotheca** Schaudinn. Amoeboid; spherical or hemispherical, being flattened on the attached surface; a thin pseudochitinous test with foreign bodies, especially sand grains; pseudopodia anastomosing; salt water.

M. arenilega S. (Fig. 149, d). Test yellow, with loosely attached foreign bodies; cytoplasm bright red due to the presence of highly refractile granules; 1–2 nuclei, 39–75 μ in diameter; body diameter 160–560 μ .

Genus **Dactylosaccus** Rhumbler. Test sausage-shape and variously twisted; pseudopodia filiform, anastomosing; salt water.

D. vermiformis R. (Fig. 149, e). Test smooth; pseudopodia arise from small finger-like projections; 1–2 nuclei; body 4 mm. by 340 μ ; salt water.

Genus **Boderia** Wright. Body form changeable; often spherical, but usually flattened and angular; filopodia long; test extremely delicate, colorless; salt water.

B. turneri W. (Fig. 149, f). Body brown to orange; active cytoplasmic movement; 1–10 nuclei; multiple division (?); 1.56–6.25 mm. in diameter; in shallow water.

Family 2 Arcellidae Schultze

Genus **Arcella** Ehrenberg. Test transparent, chitinous, densely punctated; colorless to brown (when old); in front view circular, angular, or stellate; in profile plano-convex or hemispherical; variously ornamented; aperture circular, central, inverted like a funnel; protoplasmic body does not fill the test and connected with the latter by many ectoplasmic strands; slender lobopodia,

few, digitate, simple or branched; 2 nuclei; several contractile vacuoles; fresh water. Numerous species.

A. vulgaris E. (Fig. 150, a, b). Height of test about $1/2$ the diameter; dome of hemispherical test evenly convex; aperture circular, central; colorless, yellow, or brown; protoplasmic body conforms with the shape of, but does not fill, the test; lobopodia hyaline; 2 vesicular nuclei; several contractile vacuoles; test $30\text{--}100\mu$ in diameter; in the ooze and vegetation in stagnant water

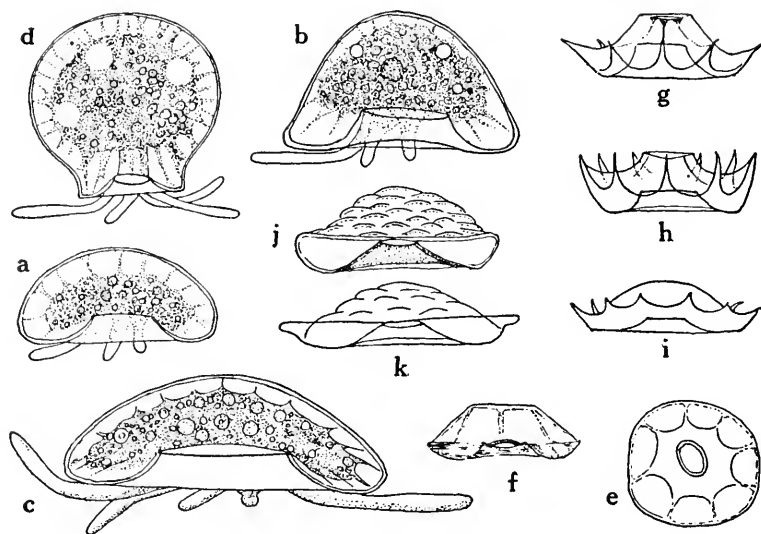


FIG. 150. a, b, *Arcella vulgaris*, $\times 170$; $\times 230$ (Leidy); c, *A. discoides*, $\times 170$ (Leidy); d, *A. mitrata*, $\times 140$ (Leidy); e, f, *A. catinus*, $\times 170$ (Cash); g-i, *A. dentata*, $\times 170$ (Leidy); j, k, *A. artocrea*, $\times 170$ (Leidy).

and also in soil. Of several varieties, two may here be mentioned: var. *angulosa* (Perty), test smaller, $30\text{--}40\mu$ in diameter, faceted, forming a 5- to 8-sided figure, with obtuse angles; var. *gibbosa* (Penard), test gibbous, surface pitted with circular depressions of uniform dimensions; $45\text{--}50\mu$ up to 100μ in diameter.

A. discoides E. (Fig. 150, c). Test circular in front view, plano-convex in profile; diameter about 3-4 times the height; test coloration and body structure similar to those of *A. vulgaris*; test $70\text{--}260\mu$ in diameter; in fresh water.

A. mitrata Leidy (Fig. 150, d). Test balloon-shaped or polyhedral; height exceeds diameter of base; aperture circular, crenu-

lated and usually everted within inverted funnel; protoplasmic body spheroidal, with 'neck' to aperture and cytoplasmic strands to test; 6 or more slender lobopodia; test 100–145 μ high, 100–152 μ in diameter; in fresh water among vegetation.

A. catinus Penard (Fig. 150, *e, f*). Test oval or quadrate, not circular, in front view; aperture oval; dome compressed; lateral margins with 6 or 8 facets; test 100–120 μ in diameter and about 45 μ high; fresh water among vegetation.

A. dentata Ehrenberg (Fig. 150, *g-i*). Test circular and dentate in front view, crown-like in profile; diameter more than twice the height; aperture circular, large; colorless to brown; about 95 μ in diameter, aperture 30 μ in diameter; 15–17 spines; in the ooze of freshwater ponds.

A. artocrea Leidy (Fig. 150, *j, k*). Height of test 1/4–1/2 the diameter; dome convex; surface mamillated or pitted; border of test everted and rising 1/4–1/2 the height of test; about 175 μ in diameter; fresh water.

Genus **Pyxidicula** Ehrenberg. Test patelliform; rigid, transparent, punctate; aperture circular, almost the entire diameter of test; cytoplasm similar to that of *Arcella*; a single nucleus; 1 or more contractile vacuoles; fresh water.

P. operculata (Agardh) (Fig. 151, *a, b*). Test smooth, colorless to brown; a single vesicular nucleus; pseudopodia short, lobose or digitate; 20 μ in diameter; on vegetation.

Genus **Pseudochlamys** Claparède et Lachmann. Test discoid, flexible when young; body with a central nucleus and several contractile vacuoles.

P. patella C. et L. (Fig. 151, *c*). Young test hyaline, older one rigid and brown; often rolled up like a scroll; a short finger-like pseudopodium between folds; 40–45 μ in diameter; in fresh water among vegetation, in moss and soil.

Genus **Diffugiella** Cash. Test ovoid, not compressed, flexible and transparent membrane; colorless cytoplasm fills the test, usually with chlorophyllous food material; median pseudopodia lobate or digitate with aciculate ends, while lateral pseudopods long, straight, and fine, tapering to a point; fresh water. One species.

D. apiculata C. (Fig. 151, *d, e*). About 40 μ by 28 μ ; among vegetation.

Genus **Cryptodiffugia** Penard. Small test yellowish to brown-

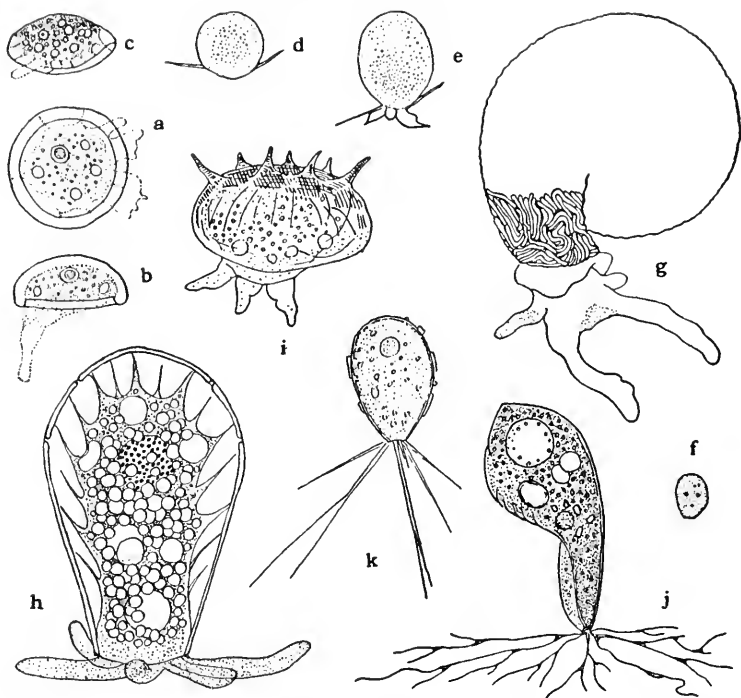


FIG. 151. a, b, *Pyxidicula operculata*, $\times 800$ (Penard); c, *Pseudochlamys patella*, $\times 330$ (Cash); d, e, *Diffugiella apiculata*, $\times 270$ (Cash); f, *Cryptodiffugia oviformis*, $\times 320$ (Cash); g, *Lesquereusia spiralis*, $\times 270$ (West); h, *Hyalosphenia papilio*, $\times 330$ (Leidy); i, *Corycia coronata*, $\times 170$ (Penard); j, *Pamphagus mutabilis*, $\times 330$ (Leidy); k, *Plagiophrys parvipunctata*, $\times 330$ (Penard).

ish; Diffugia-like in general appearance, compressed; with or without foreign bodies; pseudopodia long, acutely pointed; fresh water.

C. oviformis P. (Fig. 151, f). Test ovoid; without foreign bodies; crown hemispherical; aperture truncate; cytoplasm with chlorophyllous food particles; $16-20\mu$ by $12-15\mu$; in marshy soil.

Genus **Lesquereusia** Schlumberger. Test compressed, oval or globular in profile, narrowed at bent back; semispiral in appearance; with curved or comma-shaped rods or with sand-grains (in one species); body does not fill up the test; pseudopodia simple or branched; fresh water.

L. spiralis (Ehrenberg) (Fig. 151, g). Aperture circular; border

distinct; cytoplasm appears pale yellow; a single nucleus; $96-188\mu$ by $68-114\mu$; in marsh water.

Genus **Hyalosphenia** Stein. Test ovoid or pyriform; aperture end convex; homogeneous and hyaline, mostly compressed; crown uniformly arched; protoplasm partly filling the test; several blunt pseudopodia simple or digitate. Several species.

H. papilio Leidy (Fig. 151, *h*). Test yellowish; transparent; pyriform or oblong in front view; a minute pore on each side of crown and sometimes one also in center; aperture convex; in narrow lateral view, elongate pyriform, aperture a shallow notch; with chlorophyllous particles and oil globules; $110-140\mu$ long; in fresh water among vegetation.

Genus **Corycia** Dujardin. Envelope extremely pliable, open at base, but when closed, sack-like; envelope changes its shape with movement and contraction of body; with or without spinous projections.

C. coronata Penard (Fig. 151, *i*). 6-12 spines; 140μ in diameter; in moss.

Genus **Pamphagus** Bailey. Test hyaline membranous, flexible; aperture small; body fills the envelope completely; spherical nucleus large; contractile vacuoles; filopodia long, delicate, branching, but not anastomosing; fresh water.

P. mutabilis B. (Fig. 151, *j*). Envelope $40-100\mu$ by $28-68\mu$.

Genus **Plagiophrys** Claparède et Lachmann. Envelope thin, hyaline, changeable with body form; usually elongate-oval with rounded posterior end; narrowed at other half; envelope shows fine punctuation with a few small plates; aperture round; cytoplasm clear; nucleus large; pseudopods straight filopodia, sometimes branching; fresh water.

P. parvipunctata Penard (Fig. 151, *k*). Envelope 50μ long.

Genus **Leptochlamys** West. Test ovoid, thin transparent chitinous membrane, circular in optical section; aperture end slightly expanded with a short neck; aperture circular, often oblique; body fills test; without vacuoles; pseudopodium short, broadly expanded and sometimes cordate; fresh water.

L. ampullacea W. (Fig. 152, *a*). Nucleus large, posterior; with green or brown food particles; test $45-55\mu$ by $36-40\mu$ in diameter; aperture $15-17\mu$; among algae.

Genus **Chlamydophrys** Cienkowski. Test rigid, circular in section; aperture often on drawn-out neck; body fills the test; zonal

differentiation of cytoplasm distinct, nucleus vesicular; refractile waste granules; pseudopodia branching; fresh water or coprozoic.

C. stercorea C. (Fig. 152, *k*). Test 18–20 μ by 12–15 μ ; mature cysts yellowish brown, 12–15 μ in diameter; multiplication by budding; coprozoic and fresh water.

Genus **Cochliopodium** Hertwig et Lesser. Test thin, flexible expansible and contractile; with or without extremely fine hair-like processes; pseudopodia blunt or pointed, but not acicular. Several species.

C. bilimbosum (Auerbach) (Fig. 152, *b*). Test hemispherical; pseudopodia conical with pointed ends; test 24–56 μ in diameter; fresh water among algae.

Genus **Amphizonella** Greeff. Test membranous with a double marginal contour; inner membrane smooth, well-defined; outer serrulate; aperture inverted; a single nucleus; pseudopodia blunt, digitate, and divergent.

A. violacea G. (Fig. 152, *c*). Test patelliform, violet-tinted; with chlorophyllous corpuscles and grains; sluggish; average diameter 160 μ ; fresh water.

Genus **Zonomyxa** Müsslin. Test rounded pyriform, flexible, chitinous, violet-colored; endoplasm vacuolated, with chlorophyllous particles; several nuclei; pseudopodia simple, not digitate; fresh water.

Z. violacea N. (Fig. 152, *d*). A single lobular pseudopodium with acuminate end; 4 nuclei; diameter 140–160 μ ; actively motile forms 250 μ or longer; among sphagnum.

Genus **Microcorycia** Cockerell. Test discoidal or hemispherical, flexible, with a diaphanous continuation or fringe around periphery, being folded together or completely closed; crown of test with circular or radial ridges; body does not fill the test; 1–2 nuclei; pseudopodia lobular or digitate; fresh water. A few species.

M. flava (Greeff) (Fig. 152, *e, f*). Test yellowish brown; crown with few small foreign bodies; endoplasm with yellowish brown granules; 2 nuclei; contractile vacuoles; diameter 80–100 μ ; young individuals as small as 20 μ ; in moss.

Genus **Parmulina** Penard. Test ovoid, chitinoid with foreign bodies; aperture capable of being closed, a single nucleus, 1 or more contractile vacuoles; fresh water. A few species.

P. cyathus P. (Fig. 152, *g, h*). Test small, flexible; ovoid in aper-

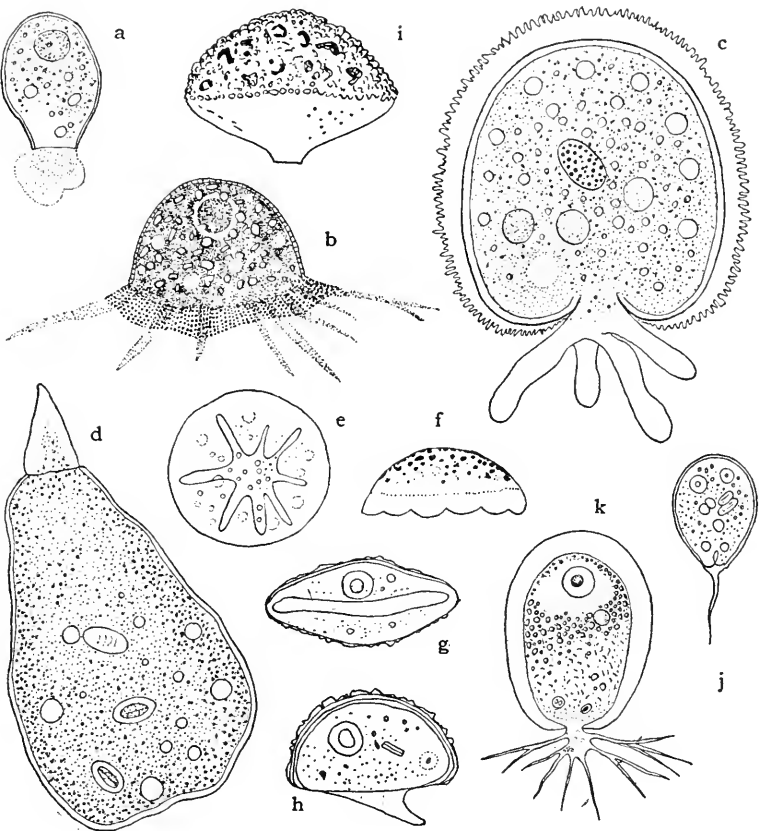


FIG. 152. a, *Leptochlamys ampullacea*, $\times 330$ (West); b, *Cochliopodium bilimbosum*, $\times 670$ (Leidy); c, *Amphizonella violacea*, $\times 270$ (Greeff); d, *Zonomyxa violacea*, $\times 200$ (Penard); e, f, *Microcorycia flava*, $\times 240$ (Wailles); g, h, *Parmulina cyathus*, $\times 500$ (Penard); i, *Capsellina timida*, $\times 270$ (Brown); j, *Diplochlamys leidyi*, $\times 270$ (Wailles); k, *Chlamydophrys stercorea*, $\times 670$ (Wenyon).

ture view, semicircular in profile; aperture a long, narrow slit when test is closed, but circular or elliptical when opened; $40\text{--}55\mu$ long; in moss.

Genus **Capsellina** Penard. Test hyaline, ovoid, membranous; with or without a second outer covering; aperture long slit; a single nucleus; 1 or more contractile vacuoles; filose pseudopodia; fresh water.

C. timida Brown (Fig. 152, i). Small, ovoid; elliptical in cross-

section; with many oil (?) globules; filopodium; 34μ by 25μ ; in moss.

Genus **Diplochlamys** Greeff. Test hemispherical or cup-shaped, flexible with a double envelope; inner envelope a membranous sack with an elastic aperture, outer envelope with loosely attached foreign bodies; aperture large; nuclei up to 100; pseudopodia few, short, digitate or pointed; fresh water. Several species.

D. leidy G (Fig. 152, *j*). Test dark gray; inner envelope projecting beyond outer aperture; nuclei up to 20 in number; diameter $80\text{--}100\mu$.

Family 3 Diffugiidae Taránek

Genus **Diffugia** Leclerc. Test variable in shape, but generally circular in cross-section; composed of cemented quartz-sand; diatoms, and other foreign bodies; aperture terminal; often with zoochlorellae; cytoplasmic body almost fills the test; a single nucleus; many contractile vacuoles; pseudopodia cylindrical, simple or branching; end rounded or pointed; fresh water, woodland soil, etc.

D. oblonga Ehrenberg (*D. pyriformis* Perty) (Fig. 153, *a*). Test pyriform, flask-shaped, or ovoid; neck variable in length; fundus rounded, with occasionally 1–3 conical processes; aperture terminal, typically circular; test composed of angular sand-grains, diatoms; bright green with chlorophyllous bodies; $60\text{--}580\mu$ by $40\text{--}240\mu$; in the ooze of freshwater ponds, ditches and bogs; also in moist soil. Several varieties.

D. urceolata Carter (Fig. 153, *b*). A large ovoid, rotund test, with a short neck and a rim around aperture; $200\text{--}230\mu$ by $150\text{--}200\mu$; in ditches, ponds, sphagnum swamps, etc.

D. arcuata Leidy (Fig. 153, *c, d*). Test hemispherical, base slightly concave, but not invaginated; aperture triangular, central, trilobed; test yellowish with scattered sand-grains or diatoms; diameter $100\text{--}140\mu$, in sphagnum swamp, moss, soil, etc.

D. lobostoma Leidy (Fig. 153, *e*). Test ovoid to subspherical; aperture terminal; with 3–6 lobes; test usually composed of sand-grains, rarely with diatoms; endoplasm colorless or greenish; diameter $80\text{--}120\mu$; in fresh water.

D. constricta (Ehrenberg) (Fig. 153, *f*). Test laterally ovoid, fundus more or less prolonged obliquely upward, rounded, and simple or provided with spines; soil forms generally spineless; aperture antero-inferior, large, circular or oval and its edge in-

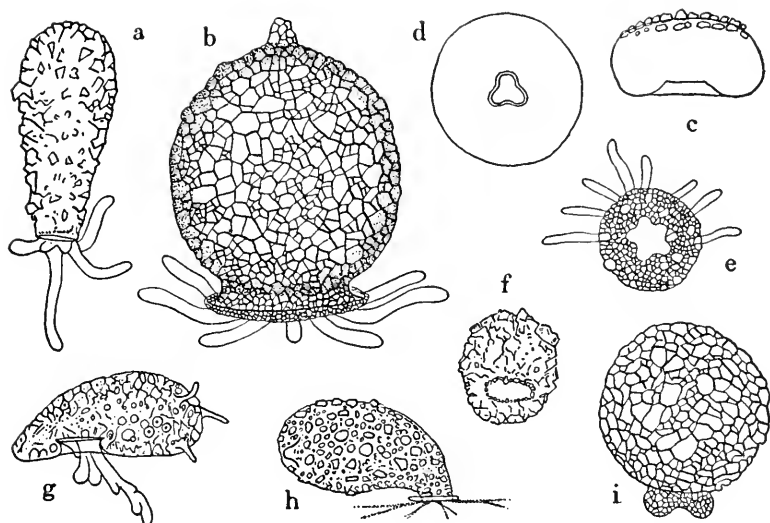


FIG. 153. a, *Diffflugia oblonga*, $\times 130$ (Cash); b, *D. urceolata*, $\times 130$ (Leidy); c, d, *D. arcuata*, $\times 170$ (Leidy); e, *D. lobostoma*, $\times 130$ (Leidy); f, *D. constricta*, $\times 200$ (Cash); g, *Centropyxis aculeata*, $\times 200$ (Cash); h, *Campascus cornutus*, $\times 170$ (Leidy); i, *Cucurbitella mespiliformis*, $\times 200$ (Wailles).

verted; test composed of quartz grains; colorless to brown; cytoplasm colorless; $80\text{--}340\mu$ long; in the ooze of ponds and in soil.

D. corona Wallich. Test ovoid to spheroid, circular in cross-section; crown broadly rounded, with a variable number of spines, aperture more or less convex in profile, central and its border multidentate or multilobate; test with fine sand-grains, opaque; cytoplasm colorless; pseudopodia numerous, long, branching or bifurcating; $180\text{--}230\mu$ by about 150μ ; in fresh water.

Genus **Centropyxis** Stein. Test circular, ovoid, or discoid; aperture eccentric, circular or ovoidal, often with a lobate border; with or without spines; cytoplasm colorless; pseudopodia digitate; fresh water.

C. aculeata S. (Fig. 153, g). Test variable in contour and size; with 4–6 spines; opaque or semitransparent; with fine sand-grains or diatom shells; pseudopodia sometimes knotted or branching; when eneysted, the body assumes a spherical form in wider part of test; granulated, colorless or with green globules; diameter $100\text{--}150\mu$; aperture $50\text{--}60\mu$ in diameter.

Genus **Campascus** Leidy. Test retort-shaped with curved neck,

rounded triangular in cross-section; aperture circular, oblique, with a thin transparent discoid collar; nucleus large; 1 or more contractile vacuoles; body does not fill the test; fresh water.

C. cornutus L. (Fig. 153, *h*). Test pale-yellow, retort-form; with a covering of small sand particles; triangular in cross-section; a single nucleus and contractile vacuole; filopodia straight; 110–140 μ long; aperture 24–28 μ in diameter; in the ooze of mountain lakes.

Genus **Cucurbitella** Penard. Test ovoid with sand grains, not compressed; aperture terminal, circular, surrounded by a 4-lobed annular collar; cytoplasm grayish, with zoochlorellae; nucleus large; 1 to many contractile vacuoles; pseudopodia numerous, digitate; fresh water.

C. mespiliformis P. (Fig. 153, *i*). 115–140 μ long; diameter 80–105 μ ; in the ooze or on vegetation in ponds and ditches.

Genus **Plagiopyxis** Penard. Test subcircular in front view; ovoid in profile; aperture linear or lunate; cytoplasm gray, with a single nucleus and a contractile vacuole; fresh water.

P. callida P. (Fig. 154, *a*). Test gray, yellowish, or brown; large nucleus vesicular; pseudopodia numerous, radiating, short, pointed or palmate; diameter 55–135 μ ; in vegetation.

Genus **Pontigulasia** Rhumbler. Test similar to that of *Diffugia*, but with a constriction of neck and internally a diaphragm made of the same substances as those of the test.

P. vas (Leidy) (Fig. 154, *b*). Round or ovoid test; constriction deep and well-marked; with sand-grains and other particles; aperture terminal; 125–170 μ long; fresh water ponds.

Genus **Phryganella** Penard. Test spheroidal or ovoid, with sand-grains and minute diatom shells; aperture terminal, round; pseudopodia drawn out to a point; fresh water.

P. acropodia (Hertwig et Lesser) (Fig. 154, *c*). Test circular in aperture view; hemispherical in profile; yellowish or brownish, semi-transparent, and covered with sand-grains and scales; in front view sharply pointed pseudopodia radiating; colorless endoplasm usually with chlorophyllous bodies; 30–50 μ in diameter.

Genus **Bullinula** Penard. Test ellipsoidal, flattened on one face, with silicious plates; on the flattened surface, ∞ -shaped aperture; a single nucleus; pseudopodia digitate or spatulate, simple or branched; fresh water.

B. indica P. (Fig. 154, *d*). Test dark brown; 120–250 μ in diameter.

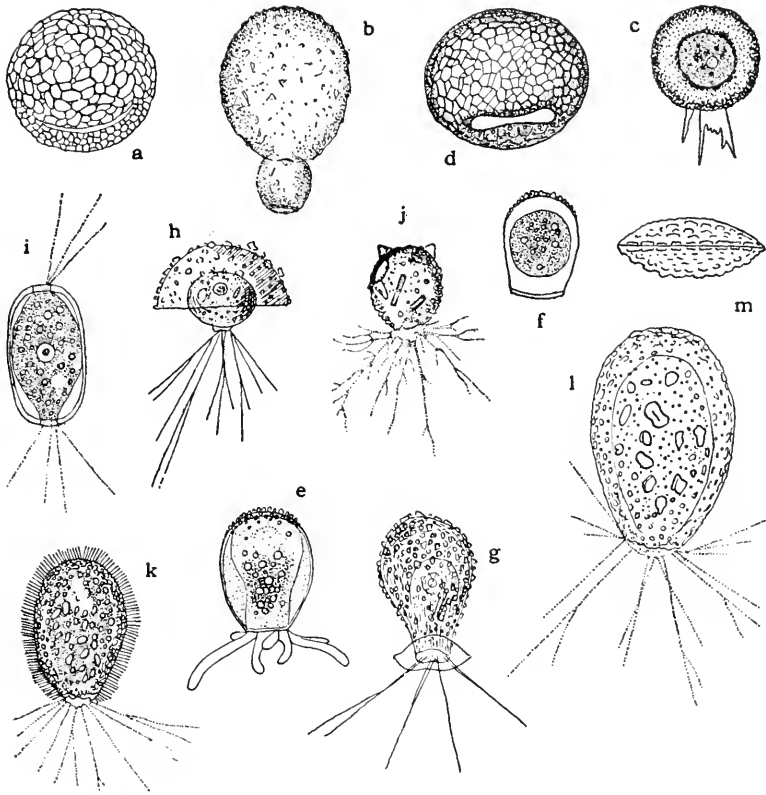


FIG. 154. a, *Plagiopyxis callida*, $\times 200$ (Wailles); b, *Pontigulasia vas*, $\times 200$ (Cash); c, *Phryganella acropodia*, $\times 190$ (Cash); d, *Bullinula indica*, $\times 130$ (Wailles); e, f, *Heleopera petricola*, $\times 190$ (Cash); g, *Nadinella tenella*, $\times 400$ (Penard); h, *Frenzelina reniformis*, $\times 600$ (Penard); i, *Amphitrema flavum*, $\times 360$ (Cash and Wailles); j, *Pseudodifflugia gracilis*, $\times 330$ (Cash); k, *Diaphoropodon mobile*, $\times 270$ (Cash and Wailles); l, m, *Clypeolina marginata*, $\times 330$ (Cash and Wailles).

Genus **Heleopera** Leidy. Test variously colored; fundus hemispherical, with sand-grains; surface covered with amorphous scales, often overlapping; aperture truncate, narrow, elliptic notched in narrow lateral view; a single nucleus; pseudopodia variable in number, thin, digitate or branching; fresh water. Several species.

H. petricola L. (Fig. 154, e, f). Test variable in size and color, strongly compressed; fundus rough with sand-grains of various

sizes; aperture linear or elliptic, convex in front view; pseudopodia slender, branching; $80\text{--}100\mu$ long; in boggy places.

Genus **Averintzia** Schouteden. Test similar to that of *Heleopera*, but small aperture elliptical; test thickened around aperture; fresh water.

A. cyclostoma (Penard). Test dark violet, with sand-grains of different sizes; elliptical in cross-section; pseudopodia unobserved; $135\text{--}180\mu$ long; in sphagnum and other aquatic plants.

Genus **Nadinella** Penard. Test chitinous, thin, hyaline, with foreign bodies and collar around aperture; filopodia; fresh water.

N. tenella P. (Fig. 154, *g*). $50\text{--}55\mu$ long; fresh water lakes.

Genus **Frenzelina** Penard. Two envelopes, outer envelope hemispherical, thin, rigid, covered with siliceous particles; inner envelope round or ovoid, drawn out at aperture, thin, hyaline and covering the body closely; aperture round, through which a part of body with its often branching straight filopods, extends; cytoplasm with diatoms, etc.; a nucleus and a contractile vacuole; fresh water.

F. reniformis P. (Fig. 154, *h*). Outer envelope $26\text{--}30\mu$ in diameter; fresh water lakes.

Genus **Amphitrema** Archer. Test ovoid, symmetrical, compressed; composed of a transparent membrane, with or without adherent foreign bodies; 2 apertures at opposite poles; with zoochlorellae; nucleus central; 1—several contractile vacuoles; straight filopodia, sparsely branched, radiating; fresh water. Several species.

A. flavum A. (Fig. 154, *i*). Test brown, cylindrical with equally rounded ends in front view; elliptical in profile; ovoid with a small central oval aperture in end-view; $45\text{--}77\mu$ by $23\text{--}45\mu$; in sphagnum.

Genus **Pseudodiffugia** Schlumberger. Test ovoid, usually rigid, with foreign bodies; circular or elliptical in cross-section; aperture terminal; granulated cytoplasm colorless or greyish; nucleus posterior; a contractile vacuole; filopodia long, straight or branching; fresh water. Several species.

P. gracilis S. (Fig. 154, *j*). Test yellowish or brownish; subspherical, with sand-grains; aperture without neck; $20\text{--}65\mu$ long.

Genus **Diaphoropodon** Archer. Test ovoid, flexible, with minute foreign bodies and a thick covering of hyaline hair-like projections; pseudopodia long, filose, branching; fresh water.

D. mobile A. (Fig. 154, *k*). Test brown; of various shapes; aperture terminal; body does not fill the test; nucleus large; 1–2 contractile vacuoles; 60–120 μ long; projections 8–10 μ long; in vegetation.

Genus **Clypeolina** Penard. Test ovoid, compressed, formed of a double envelope; outer envelope composed of 2 valves with scales and particles; inner envelope a membranous sack; long filopodia, often branching; fresh water.

C. marginata P. (Fig. 154, *l, m*). Outer test-valves yellow to dark brown; lenticular in cross-section; wide terminal aperture; endoplasm with many small globules; a single nucleus and contractile vacuole; 80–150 μ long.

Family 4 **Euglyphidae** Wallich

Genus **Euglypha** Dujardin (*Pareuglypha* Penard). Test hyaline, ovoid, composed of circular, oval, or scutiform siliceous imbricated scales, arranged in longitudinal rows; aperture bordered with regularly arranged denticulate scales; usually with spines; 1–2 nuclei large, placed centrally; filopodia dichotomously branched; contractile vacuoles; fresh water. Numerous species.

E. acanthophora (Ehrenberg) (*E. alveolata* D.) (Fig. 67). Test ovoid, or slightly elongate; 3–7 scales protruding around the circular aperture; scales elliptical; body almost fills the test; 50–100 μ long.

E. cristata Leidy (Fig. 155, *a*). Test small, elongate with a long neck, fundus with 3–8 spines; scales oval; aperture circular, bordered by a single row of 5–6 denticulate scales; cytoplasm colorless; nucleus posterior; reserve scales are said to be collected around the exterior of aperture, unlike other species in which they are kept within the cytoplasm; 30–70 μ long; 12–23 μ in diameter; aperture 6–12 μ ; scales 4.5–9.5 μ by 2.5–6.5 μ ; spines 10–15 μ long.

E. mucronata L. (Fig. 155, *b*). Test large; fundus conical, with 1–2 terminal spines (12–44 μ long); aperture circular, bordered by a single row of 6–8 denticulate scales; 100–150 μ long, diameter 30–60 μ ; aperture 15–20 μ in diameter.

Genus **Paulinella** Lauterborn. Test small ovoid, not compressed; with siliceous scales in alternating transverse rows; aperture terminal; body does not fill the test completely; nucleus posterior; among vegetation in fresh or brackish water.

P. chromatophora L. (Fig. 155, c). Scales arranged in 11–12 rows, 5 scales in each row; with 1–2 curved chromatophores; no food particles; a single contractile vacuole; 20–32 μ long; 14–23 μ in diameter.

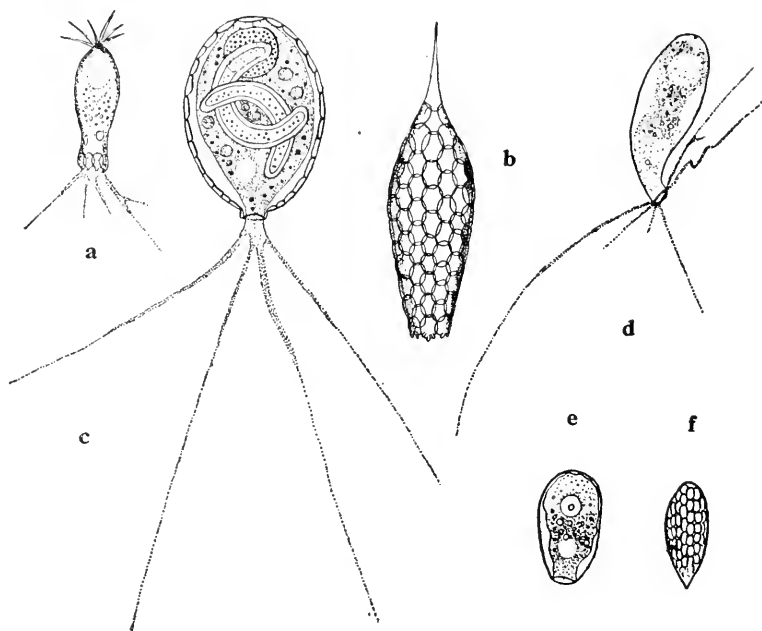


FIG. 155. a, *Euglypha cristata*, $\times 330$ (Wailes); b, *E. mucronata*, $\times 330$ (Wailes); c, *Paulinella chromatophora*, $\times 1000$ (Wailes); d, *Cyphoderia ampulla*, $\times 200$ (Cash); e, f, *Corythion pulchellum*, $\times 350$ (Wailes).

Genus **Cyphoderia** Schlumberger. Test retort-shaped; colorless to yellow; made up of a thin chitinous membrane, covered with discs or scales; aperture terminal, oblique, circular; body does not fill the test completely; nucleus large, posterior, pseudopodia, few, long filose, simple or branched; fresh water.

C. ampulla (Ehrenberg) (Fig. 155, d). Test usually yellow, translucent, composed of discs, arranged in diagonal rows; circular in cross-section; aperture circular; cytoplasm gray, with many granules and food particles; 2 contractile vacuoles; 60–200 μ long; diameter 30–70 μ . Several varieties.

Genus **Trinema** Dujardin. Test small, hyaline, ovoid, compressed anteriorly, with circular siliceous scales; aperture circular,

oblique, invaginate; nucleus posterior; filopodia not branched; fresh water in vegetation.

T. enchelys (Ehrenberg) (Fig. 156, *a*). 1–2 contractile vacuoles; pseudopodia attenuate, radiating; 30–100 μ long; 15–60 μ wide; scales 4–12 μ in diameter.

Genus **Corythion** Taránek. Test small, hyaline, composed of small oval siliceous plates; compressed; elliptical in cross-section; aperture subterminal, ventral or oblique, and circular or oval; numerous filopodia; fresh water.

C. pulchellum Penard (Fig. 155, *e, f*). Aperture lenticular; cytoplasm colorless; 2–3 contractile vacuoles; 25–35 μ by 15–20 μ ; aperture 7–10 μ by 3–4 μ .

Genus **Placocista** Leidy. Test ovoid, hyaline, compressed; lenticular in cross-section; with oval or subcircular siliceous scales; aperture wide, linear, with flexible undulate borders; nucleus large, posterior; often with zoochlorellae; filopodia branching and many, generally arising from a protruded portion of cytoplasm; fresh water.

P. spinosa (Carter) (Fig. 156, *b*). Margin of test with spines, either singly or in pairs; 116–174 μ by 70–100 μ ; in sphagnum.

Genus **Assulina** Ehrenberg. Test colorless or brown; ovoid; with elliptical scales, arranged in diagonal rows; aperture oval, terminal, bordered by a thin chitinous dentate membrane; nucleus posterior; contractile vacuoles; filopodia divergent, sometimes branching; fresh water.

A. seminulum (E.) (Fig. 156, *c*). Body does not fill the test; with numerous food particles; pseudopodia few, straight, divergent, slender, seldom branched; 60–150 μ by 50–75 μ ; in sphagnum.

Genus **Nebela** Leidy. Test thin, ovate or pyriform; with circular or oval platelets of uniform or various sizes; highly irregular; endoplasm with oil-globules; nucleus posterior; body does not fill the test, and is connected with the latter by many ectoplasmic strands at fundus end; pseudopodia blunt, rarely branched; fresh water. Numerous species.

N. collaris (Ehrenberg) (Fig. 156, *d*). Test pyriform, fundus obtuse in profile; aperture without any notch; endoplasm with chlorophyllous food particles; pseudopodia digitate, short, usually 3–6 in number; about 130 μ by 85–90 μ ; in marshes among sphagnum.

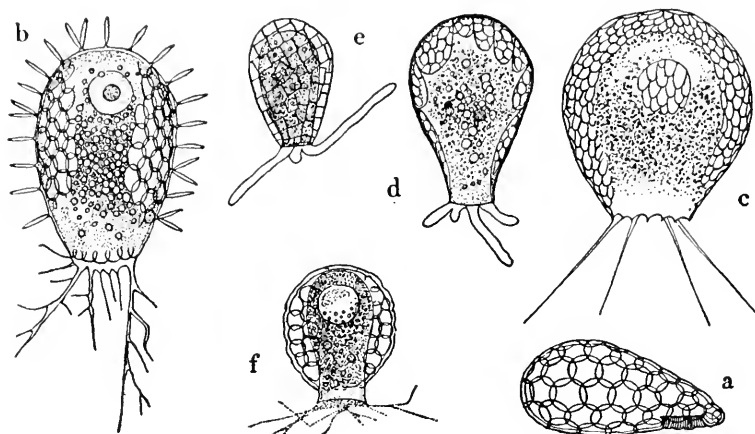


FIG. 156. a, *Trinema enchelys*, $\times 330$ (Wailles); b, *Placocista spinosa*, $\times 200$ (Wailles); c, *Assulina seminulum*, $\times 400$ (Wailles); d, *Nebela collaris*, $\times 200$ (Cash); e, *Quadrula symmetrica*, $\times 200$ (Cash); f, *Sphegnoderia lenta*, $\times 330$ (Leidy).

Genus **Quadrula** Schulze. Test pyriform, hemispherical, or discoidal; with quadrangular siliceous or calcareous platelets, arranged generally in oblique series, not overlapping; a single nucleus; body and pseudopodia similar to those of *Diffugia*; fresh water.

Q. symmetrica (Wallich) (Fig. 156, e). Compressed, smaller platelets near aperture; cytoplasm very clear, with chlorophyllous granules; 3–5 pseudopodia digitate; nucleus posterior; $80\text{--}140\mu$ by $40\text{--}96\mu$; in sphagnum.

Genus **Sphegnoderia** Schlumberger. Test globular or oval, sometimes slightly compressed; hyaline, membranous, with a short broad neck, and a wide elliptical aperture; scales circular, oval, or hexagonal, arranged in alternating series; cytoplasm colorless; 1–2 contractile vacuoles; filopodia, fine, branching; fresh water.

S. lenta S. (Fig. 156, f). Hyaline test ovoid or globular; scales circular or broadly oval; aperture terminal, surrounded by a thin chitinous collar, one side inclined inwards; nucleus large; cytoplasm colorless; 2 contractile vacuoles; $30\text{--}64\mu$ by $20\text{--}46\mu$; aperture $10\text{--}22\mu$ in diameter.

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CHAPTER 20

Order 5 Foraminifera d'Orbigny

THE Foraminifera are comparatively large Protozoa, living almost exclusively in the sea. They were very abundant in geologic times and the fossil forms are important in applied geology (p. 9). The majority live on ocean bottom, moving about sluggishly over the mud and ooze by means of their pseudopodia. Some are attached to various objects on the ocean floor, while others are pelagic.

The cytoplasm is ordinarily not differentiated into the two zones and streams out through the apertures, and in perforated forms through the numerous pores, of the shell, forming rhizopodia which are fine and often very long and which anastomose with one another to present a characteristic appearance (Fig. 5). The streaming movement of the cytoplasm in the pseudopodia are quite striking; the granules move toward the end of a pseudopodium and stream back along its periphery. The body cytoplasm is often loaded with brown granules which are apparently waste matter and in some forms such as *Peneroplis pertusus* (Fig. 160), these masses are extruded from the body from time to time, especially prior to the formation of a new chamber. Contractile vacuoles are usually not found in the Foraminifera.

The test of the Foraminifera varies greatly in form and structure. When alive, it may show various colorations—orange, red, or brown. The majority measure less than one millimeter, although larger forms may frequently reach several millimeters. The test may be siliceous or calcareous and in some forms, various foreign materials, such as sand-grains, sponge-spicules, etc. which are more or less abundantly found where these organisms live, are loosely or compactly cemented together by pseudochitinous or gelatinous substances. Certain forms show a specific tendency in the selection of foreign materials for the test (p.38-39). Siliceous tests are comparatively rare, being found in some species of Miliolidae inhabiting either the brackish water or deep sea. Calcareous tests are sometimes imperforated, but even in such cases those of the young are always perforated. By far the majority of the Foraminifera possess perforated calcareous tests. The

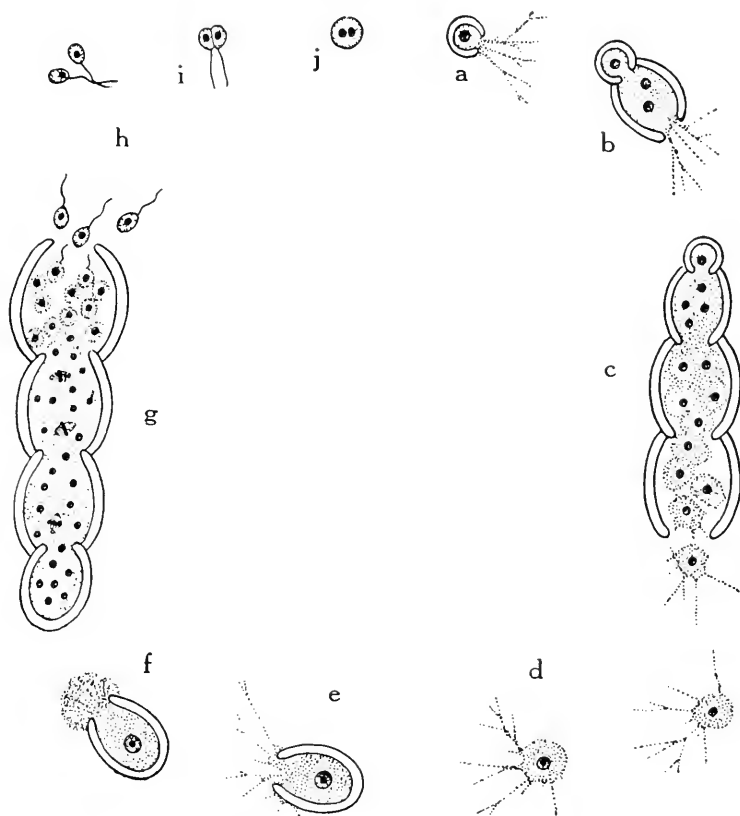


FIG. 157. Diagram illustrating the life-cycle of Foraminifera (Kühn). a-c, microspheric generation; d, uninucleate phase; e-g, megalospheric generation; h, isogametes; i-j, isogamy.

thickness of shell varies considerably, as do also the size and number of apertures, among different species. Frequently the perforations are very small in the young and later become large and coarse, while in others the reverse may be the case.

The form of shell varies greatly. In some there is only one chamber, composed of a central body and radiating arms which represent the material collected around the pseudopodia, as in *Rhabdammina* (Fig. 158, a), or of a tubular body alone, as in *Hyperammina* (Fig. 158, d). The polythalamous forms possess shells of various spirals. The first chamber is called the **proloculum** which may be formed either by the union of two swimmers or

by asexual reproduction (Fig. 157). The former is ordinarily small and known as the **microspheric** proloculum (*a*), while the latter, which is usually large, is called the **megalospheric** proloculum (*e*). To the proloculum are added many chambers which may be closely or loosely coiled or not coiled at all. These chambers are ordinarily undivided, but in many higher forms they are divided into chamberlets. The chambers are delimited by the suture on the exterior of the shell. The septa which divide the chambers are perforated by one or more foramina known as stolon canals, through which the protoplasm extends throughout the chambers. The last chamber has one or more apertures of variable sizes, through which the cytoplasm extends to the exterior as pseudopodia. The food of Foraminifera consists mostly of diatoms and algae, though pelagic forms are known to capture other Protozoa and microcrustaceans.

All species of Foraminifera manifest a more or less distinct tendency toward a dimorphism: the megalospheric form with a large proloculum and the microspheric form with a small proloculum (Fig. 157). The former is said to be much more numerous than the latter. The microspheric form is multinucleate, in which the nuclei are scattered without apparent order, and vary in size proportionately with the size of the chambers. As the animal grows the nuclei increase in number; around each of them a small island of cytoplasm becomes condensed (*c*); uninucleate bodies thus formed leave the parent body, and each secretes around itself a shell which is much larger than the proloculum of the parent individual (*d*, *e*). To this proloculum, are added new chambers one by one, as the organism grows (*f*) and at the same time the single nucleus shifts its position, so that the latter is almost always in the middle chamber. As the animal grows further, endosomes appear in increasing numbers in the nucleus which divides finally into many nuclei (*g*). Each of these nuclei becomes the center of swarmer. The swarmers leave the parent shell and undergo fusion in pairs to produce zygotes (*h-j*). The zygote secretes a shell around itself (*a*) and forms first a small proloculum, to which are added many chambers (*b*). This is the microspheric form which in some species appears to be unknown.

More than 300 genera of extinct and living Foraminifera are now known. Cushman distinguished 45 families. The present work follows Cushman in recognizing and differentiating 44 fami-

lies, and lists one genus as an example for each, but places *Gromia* and allied genera in the order Testacea (p. 323).

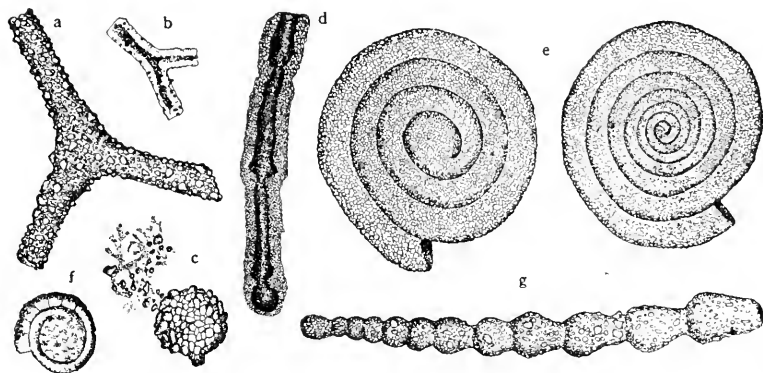


FIG. 158. a, *Rhabdammina abyssorum*, $\times 5$ (Kühn); b, *Rhizammina algaeformis*, fragment of, $\times 14$ (Cushman); c, *Saccammina sphaerica*, $\times 8$ (Rhumbler); d, *Hyperammina subnodosa*, $\times 4$ (Brady); e, *Ammodiscus incertus*, $\times 20$ (Kühn); f, *Silicina limitata*, $\times 13$ (Cushman); g, *Reophax nodulosus*, $\times 3$ (Brady).

Test entirely or in part arenaceous

Test single-chambered or rarely an irregular group of similar chambers loosely attached

Test with a central chamber, 2 or more arms; fossil and recent
..... Family 1 Astorhizidae

Genus *Rhabdammina* Sars (Fig. 158, a)

Test without a central chamber, elongate, open at both ends;
fossil and recent..... Family 2 Rhizamminidae

Genus *Rhizammina* Brady (Fig. 158, b)

Test a chamber or rarely series of similar chambers loosely attached, with normally a single opening; fossil and recent...
..... Family 3 Saccamminidae

Genus *Saccammina* Sars (Fig. 158, c)

Test 2-chambered, a proloculum and long undivided tubular second chamber

Test with the second chamber, simple or branching, not coiled;
mostly recent and also fossil... Family 4 Hyperamminidae

Genus **Hyperammina** Brady (Fig. 158, *d*)

- Test with the second chamber usually coiled at least in young
 Test of arenaceous material with much cement, usually yellowish or reddish brown; fossil and recent.
 Family 5 Ammodiscidae

Genus **Ammodiscus** Reuss (Fig. 158, *e*)

- Test of siliceous material, second chamber partially divided; fossils only. Family 6 Silicinidae

Genus **Silicina** Bornemann (Fig. 158, *f*)

- Test typically many-chambered
 Test with all chambers in a rectilinear series; fossil and recent.
 Family 7 Reophaeidae

Genus **Reophax** Montfort (Fig. 158, *g*)

- Test planispirally coiled at least in young
 Axis of coil, short; many uncoiled forms; fossil and recent.
 Family 8 Lituolidae

Genus **Lituola** Lamarck (Fig. 159, *a*)

- Axis of coil usually long, all close-coiled
 Interior not labyrinthic; fossil only. Family 9 Fusulinidae

Genus **Fusulina** Fisher (Fig. 159, *b*)

- Interior labyrinthic; fossil only. Family 10 Loftusiidae

Genus **Loftusia** Brady

- Test typically biserial at least in young of microspheric form; fossil and recent. Family 11 Textulariidae

Genus **Textularia** DeFrance (Fig. 159, *c*)

- Test typically triserial at least in young of microspheric form
 Aperture usually without a tooth, test becoming simpler in higher forms; fossil and recent. Family 12 Verneulinidae

Genus **Verneulina** d'Orbigny (Fig. 159, *d*)

- Aperture typically with a tooth, test becoming conical in higher forms; fossil and recent. Family 13 Valvulinidae

Genus **Valvulina** d'Orbigny (Fig. 159, *e*)

- Test with whole body labyrinthic, large, flattened, or cylindrical; recent. Family 14 Neusiniidae

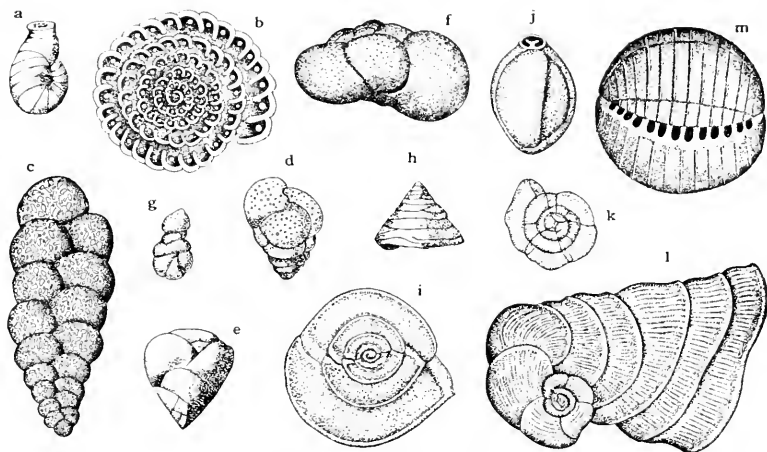


FIG. 159. a, *Lituola nautiloidea* (Cushman); b, section through a *Fusulina* (Carpenter); c, *Textularia agglutinans*, $\times 90$ (Rhumbler); d, *Verneuilina propinqua*, $\times 8$ (Brady); e, *Valvulina triangularis*, (d'Orbigny); f, *Trochammina inflata*, $\times 32$ (Brady); g, *Placopsilina cenomana* (Reuss); h, *Tetrataxis palaeotrochus*, $\times 15$ (Brady); i, *Spiroloculina limbata*, $\times 20$ (Brady); j, *Triloculina trigonula*, $\times 15$ (Brady); k, *Fischerina helix*, $\times 32$ (Heron-Allen and Earland); l, *Vertebralina striata*, $\times 40$ (Kühn); m, *Alveolinella mello*, $\times 35$ (Brady).

Genus **Neusina** Goës

Test trochoid at least while young

Mostly free; typically trochoid throughout; fossil and recent.

..... Family 15 Trochamminidae

Genus **Trochammina** Parker et Jones (Fig. 159, f)

Attached; young trochoid, later stages variously formed; fossil and recent.

..... Family 16 Placopsilinae

Genus **Placopsilina** d'Orbigny (Fig. 159, g)

Free; conical, mostly of large size; fossil only.

..... Family 17 Orbitolinidae

Genus **Tetrataxis** Ehrenberg (Fig. 159, h)

Test coiled in varying planes, wall imperforate, with arenaceous portion only on the exterior; fossil and recent.

..... Family 18 Miliolidae (in part)

Genus **Spiroloculina** d'Orbigny (Fig. 159, *i*)

Test calcareous, imperforate, porcellanous

Test with chambers coiled in varying planes, at least in young;
aperture large, toothed; fossil and recent.....

.....Family 18 Miliolidae (in part)

Genus **Triloculina** d'Orbigny (Fig. 159, *j*)

Test trochoid; fossil and recent.....Family 19 Fischerinidae

Genus **Fischerina** Terquem (Fig. 159, *k*)

Test planispiral at least in young

Axis very short, chambers usually simple; fossil and recent.....

.....Family 20 Ophthalmididae

Genus **Vertebralina** d'Orbigny (Fig. 159, *l*)

Axis short, test typically compressed and often discoid, chambers
mostly with many chamberlets; fossil and recent.....

.....Family 21 Peneroplidae

Genus **Peneroplis** Montfort (Figs. 4; 160)

Axis typically elongate, chamberlets developed; mainly fossil...

.....Family 22 Alveolinellidae

Genus **Alveolinella** Douvillé (Fig. 159, *m*)

Test globular, aperture small, not toothed; recent only.....

.....Family 23 Keramosphaeridae

Genus **Keramosphaera** Brady

Test calcareous, perforate

Test vitreous with a glassy lustre, aperture typically radiate, not
trochoid

Test planispirally coiled or becoming straight, or single-cham-
bered; fossil and recent.....Family 24 Lagenidae

Genus **Lagena** Walker et Jacob (Fig. 161, *a*)

Test biserial or elongate spiral; fossil and recent.....

.....Family 25 Polymorphinidae

Genus **Polymorphina** d'Orbigny

Test not vitreous; aperture not radiating

Test planispiral, occasionally trochoid, then usually with proc-
esses along the suture lines, septa single, no canal system;
fossil and recent.....Family 26 Nonionidae

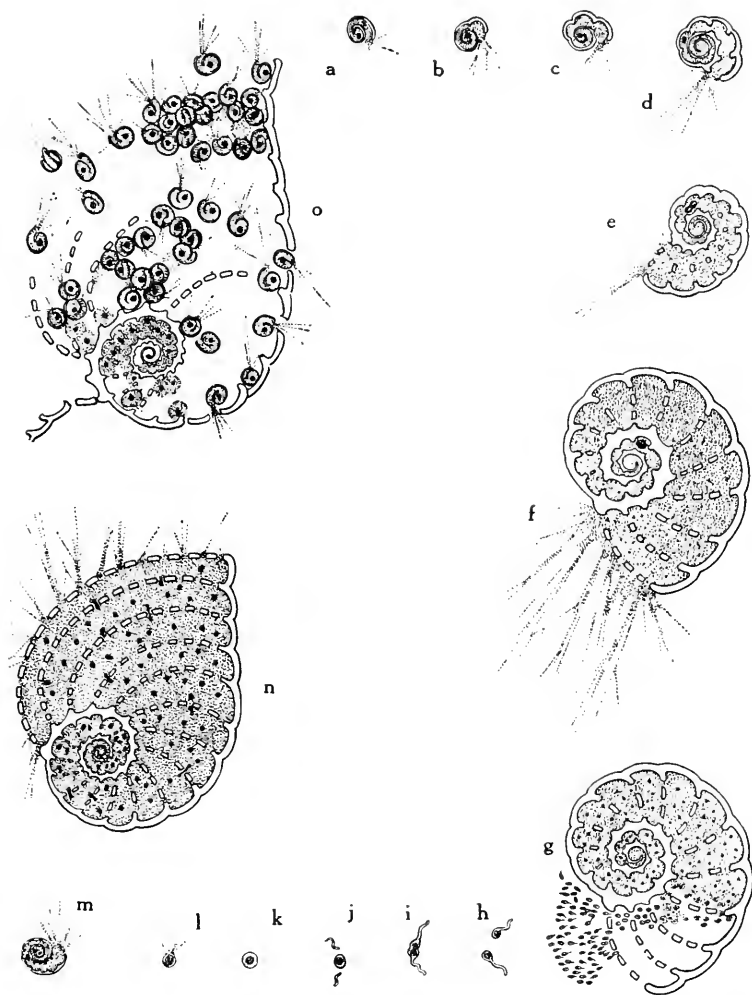


FIG. 160. Diagram illustrating the life-cycle of *Peneroplis pertusus* (Winter). a-f, megalospheric generation; g, gamete formation; h-k, isogamy; l-n, microspheric generation; o, multiple division.

Genus **Elphidium** Montfort (Figs. 5; 161, b)
(*Polystomella* Lamarck)

Test planispiral, at least in young, generally lenticular, septa double, canal system in higher forms; fossil and recent. . . .

. Family 27 Camerinidae

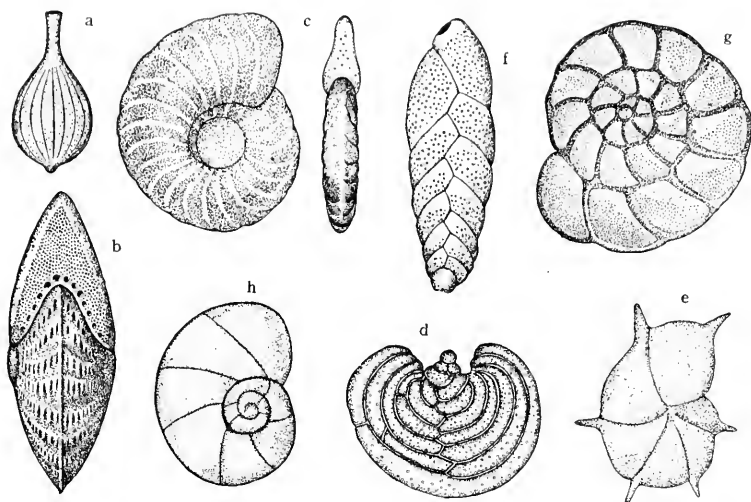


FIG. 161. a, *Lagena striata*, $\times 50$ (Rhumbler); b, *Elphidium strigilata*, $\times 40$ (Kühn); c, *Operculina ammonoides*, $\times 50$ (Kühn); d, *Pavonina flabelliformis*, $\times 30$ (Brady); e, *Hantkenina alabamensis*, $\times 40$ (Cushman); f, *Bolivina punctata*, $\times 100$ (Kühn); g, *Rotalia beccarii*, $\times 40$ (Kühn); h, *Asterigerina carinata*, $\times 30$ (d'Orbigny from Kühn).

Genus **Operculina** d'Orbigny (Fig. 161, c)

Test generally biserial in at least microspheric form, aperture usually large, without teeth; fossil and recent. Family 28 Heterohelidae

Genus **Pavonina** d'Orbigny (Fig. 161, d)

Test planispiral, bi- or tri-serial with elongate spines and lobed aperture; fossil and recent. Family 29 Hantkeninidae

Genus **Hantkenina** Cushman (Fig. 161, e)

Test typically with an internal tube, elongate
Aperture generally loop-shaped or cribrate; fossil and recent. Family 30 Buliminidae

Genus **Bolivina** d'Orbigny (Fig. 161, f)

Aperture narrow, curved, with an overhanging portion; mostly fossil, also recent. Family 31 Ellipsoidinidae

Genus **Ellipsoidina** Seguenza

Test trochoid, at least in young of microspheric form, usually coarsely perforate; when lenticular, with equatorial and lateral chambers

Test trochoid throughout, simple; aperture ventral

No alternating supplementary chambers on ventral side;
fossil and recent..... Family 32 Rotaliidae

Genus **Rotalia** Lamarek (Fig. 161, *g*)

Alternating supplementary chambers on ventral side; fossil
and recent..... Family 33 Amphisteginidae

Genus **Asterigerina** d'Orbigny (Fig. 161, *h*)

Test trochoid and aperture ventral in young

With supplementary material and large spines, independent
of chambers; fossil and recent... Family 34 Calcarinidae

Genus **Calcarina** d'Orbigny (Fig. 162, *a*)

With later chambers in annular series or globose with multiple
apertures, but not covering earlier ones; fossil and recent
..... Family 35 Halkyardiidae

Genus **Halkyardia** Heron-Allen et Earland (Fig. 162, *b*)

With later chambers somewhat biserial; aperture elongate in
the axis of coil; fossil and recent..... Family 36 Cassidulinidae

Genus **Cassidulina** d'Orbigny (Fig. 162, *c*)

With later chambers becoming involute, very few making up
the exterior in adult; aperture typically elongate, semi-
circular; in a few species circular; fossil and recent..... Family 37 Chilostomellidae

Genus **Allomorphina** Reuss (Fig. 162, *d*)

With chambers mostly finely spinose and wall cancellated,
adapted for pelagic life, globular forms with the last
chamber completely involute; aperture umbilicate or along
the suture; fossil and recent... Family 38 Globigerinidae

Genus **Globigerina** d'Orbigny (Fig. 162, *e*)

Early chambers globigerine, later ones spreading and com-
pressed; fossil and recent... Family 39 Globorotaliidae

Genus **Globorotalia** Cushman

Test trochoid at least in young, aperture peripheral or becoming
dorsal

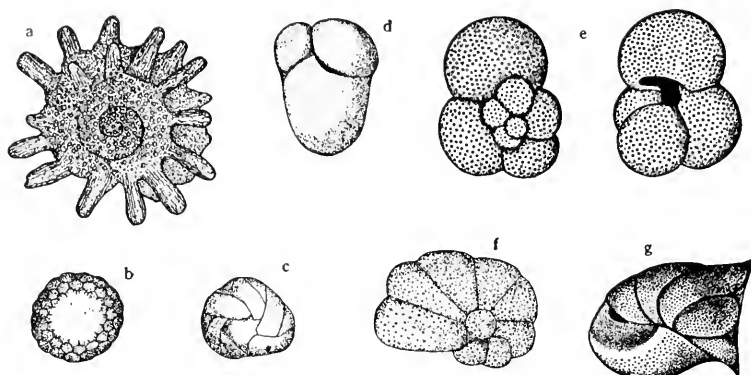


FIG. 162. a, *Calcarina defrancei*, $\times 25$ (Brady); b, *Halkyardia radiata* $\times 15$ (Cushman); c, *Cassidulina laevigata*, $\times 25$ (Brady); d, *Alломорфина trigona*, $\times 40$ (Brady); e, *Globigerina bulloides*, $\times 30$ (Kühn); f, *Anomalina punctulata* (d'Orbigny); g, *Rupertia stabilis*, $\times 50$ (Brady).

Mostly attached, dorsal side usually flattened; fossil and recent
..... Family 40 Anomalinidae

Genus **Anomalina** d'Orbigny (Fig. 162, f)

Later chambers in annular series; fossil and recent.
..... Family 41 Planorbulinidae

Genus **Planorbulina** d'Orbigny

Test trochoid in very young, later growing upward
Later chambers in a loose spiral; fossil and recent.
..... Family 42 Rupertidae

Genus **Rupertia** Wallich (Fig. 162, g)

Later chambers in masses or branching, highly colored; mostly
recent, also fossil. Family 43 Homotremidae

Genus **Homotrema** Hickson

Test trochoid in the very young of microspheric form, chambers
becoming annular later, with definite equatorial and lateral
chambers, often with pillars; fossil only.
..... Family 44 Orbitoididae

Genus **Orbitoides** d'Orbigny

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CHAPTER 21

Subclass 2 **Actinopoda** Calkins

THE Actinopoda are divided into two orders as follows:
Without central capsule Order 1 Heliozoa
With central capsule Order 2 Radiolaria (p. 367)

Order 1 **Heliozoa** Haeckel

The Heliozoa are, as a rule, spherical in form with many radiating axopodia. The cytoplasm is differentiated, distinctly in *Actinosphaerium*, or indistinctly in other species, into the coarsely vacuolated ectoplasm and the less transparent and vacuolated endoplasm. The food of Heliozoa consists of living Protozoa or Protophyta; thus their mode of obtaining nourishment is holozoic. A large organism may sometimes be captured by a group of Heliozoa which gather around the prey. When an active ciliate or a small rotifer comes in contact with an axopodium, it seems to become suddenly paralyzed and, therefore, it has been suggested that the pseudopodia contain some poisonous substances. The axial filaments of the axopodia disappear and the pseudopodia become enlarged and surround the food completely. Then the food matter is carried into the main part of the body and is digested. The ectoplasm contains several contractile vacuoles and numerous refractile granules which are scattered throughout. The endoplasm is denser and usually devoid of granules. In the axopodium, the cytoplasm undergoes streaming movements. The hyaline and homogeneous axial filament runs straight through both the ectoplasm and the endoplasm, and terminates in a point just outside the nuclear membrane. When the pseudopodium is withdrawn, its axial filament disappears completely, though the latter sometimes disappears without the withdrawal of the pseudopodium itself. In *Acanthocystis* the nucleus is eccentric (Fig. 165, *b*), but there is a central granule, or centroplast, in the center of the body from which radiate the axial filaments of the axopodia. In multinucleate *Actinosphaerium*, the axilia filaments terminate at the periphery of the endoplasm. In *Camptonema*, an axial filament arises from each of the numerous nuclei (Fig. 163, *d*).

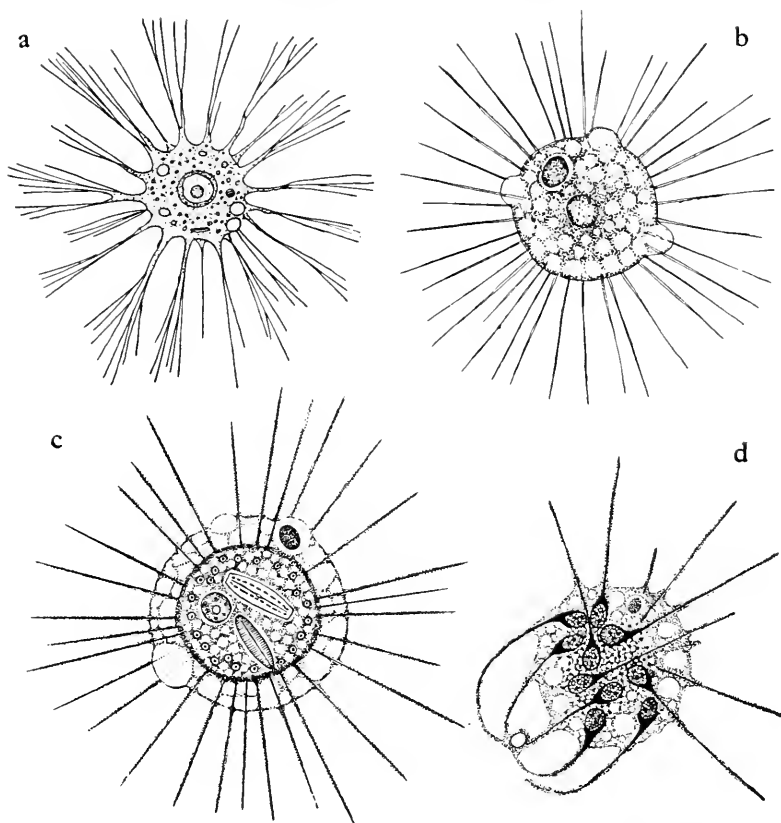


FIG. 163. a, *Actinocoma ramosa*, $\times 630$ (Penard); b, *Actinophrys sol*, $\times 400$ (Kudo); c, *Actinosphaerium eichhorni*, $\times 45$ (Kudo); d, *Camp-tonema nutans*, $\times 350$ (Schaudinn).

The skeletal structure of the Heliozoa varies among different species. The body may be naked, covered by a gelatinous mantle, or provided with a lattice-test with or without spicules. The spicules are variable in form and location and may be used for specific differentiation. In some forms there occur colored bodies bearing chromatophores, which are considered as holophytic Mastigophora (p. 24) living in the heliozoans as symbionts.

The Heliozoa multiply by binary fission or budding. Incomplete division may result in the formation of colonies, as in *Rhaphidiophrys*. In *Actinosphaerium*, nuclear phenomena have been studied by several investigators (p. 156). In *Acanthocystis*

and Oxnerella (Fig. 55), the central granule behaves somewhat like the centriole in a metazoan mitosis. Budding has been known in numerous species. In Acanthocystis the nucleus undergoes amitosis several times, thus forming several nuclei, one of which remains in place while the other migrates toward the body surface. Each peripheral nucleus becomes surrounded by a protruding cytoplasmic body which becomes covered by spicules and which is set free in the water as a bud. These small individuals are supposed to grow into larger forms, the central granules being produced from the nucleus during the growth. Formation of swarmers is known in a few genera and sexual reproduction occurs in some forms. The Heliozoa live chiefly in fresh water, although some inhabit the sea.

Without gelatinous envelope

Without flagella

Pseudopodia arise from thick basal parts, branching. Family 1 Actinocomidae

Pseudopodia not branching; cytoplasm highly vacuolated. Family 2 Actinophryidae

With 1-2 flagella. Family 3 Ciliophryidae (p. 359)

With gelatinous envelope; with or without skeleton

Without flagella

Without chitinous capsule

Without definite skeleton. . . . Family 4 Lithocollidae (p. 360)

With chitinous or siliceous spicules or scales

With chitinous spicules. . . Family 5 Heterophryidae (p. 362)

With siliceous skeleton

Cup-like plates over body; 2-3 pseudopodia often grouped. Family 6 Clathrellidae (p. 362)

Scales flattened, not cup-like. Family 7 Acanthocystidae (p. 362)

With chitinous retiform capsule. Family 8 Clathulinidae (p. 364)

With numerous flagella, among axopodia; siliceous scales. Family 9 Myriophryidae (p. 366)

Family 1 Actinocomidae Poche

Genus **Actinocoma** Penard. Body spherical; one or more contractile vacuoles; nucleus with a thick membrane, central; filopodia, not axopodia, simple or in brush-like groups; fresh water.

A. ramosa P. (Fig. 163, *a*). Average diameter 14-26 μ .

Family 2 Actinophryidae Claus

Genus **Actinophrys** Ehrenberg. Spheroidal; cytoplasm highly vacuolated, especially ectoplasm; with often symbiotic zoochlorel-

lae; nucleus central; 1- many contractile vacuoles; axopodia straight, numerous, axial filaments terminate at surface of the nucleus; "sun animalcules"; fresh water.

A. sol E. (Figs. 78; 163, b). Spherical; ectoplasm vacuolated; endoplasm granulated with numerous small vacuoles; a large central nucleus; solitary but may be colonial when young; diameter variable, average being 40-50 μ ; among plants in still fresh water. Reproduction studied by Bělař (p. 156); Looper (1928) studied its food reactions.

A. vesiculata Penard. Ectoplasm with saccate secondary vesicles, extending out of body surface between axopodia; nucleus central, with many endosomes; 25-30 μ in average diameter; fresh water.

Genus **Actinosphaerium** Stein. Spherical; ectoplasm consists almost entirely of large vacuoles in one or several layers; endoplasm with numerous small vacuoles; numerous nuclei; axial filaments end in the inner zone of ectoplasm. 2 species.

A. eichhorni Ehrenberg (Figs. 6; 163, c). Numerous nuclei scattered in the periphery of endoplasm; 2 or more contractile vacuoles, large; axial filaments arise from a narrow zone of dense cytoplasm at the border line between endoplasm and ectoplasm; body large, diameter 200-300 μ , sometimes up to 1 mm.; nuclei 12-20 μ in diameter; among vegetation in freshwater bodies.

A. arachnoideum Penard. Ectoplasm irregularly vacuolated; no distinct endoplasmic differentiation; nuclei smaller in number; pseudopodia of 2 kinds; one straight, very long and the other filiform, and anastomosing; 70-80 μ in diameter.

Genus **Camptonema** Schaudinn. Spheroidal; axial filaments of axopodia end in nuclei about 50 in number; (contractile?) vacuoles numerous and small in size; salt water.

C. nutans S. (Fig. 163, d). About 150 μ in diameter.

Genus **Oxnerella** Dobell. Spherical; cytoplasm indistinctly differentiated; eccentric nucleus with a large endosome; axial filaments take their origin in the central granule; no contractile vacuole; nuclear division typical mitosis (Fig. 55).

O. maritima D. (Fig. 55). Small, 10-22 μ in diameter; solitary, floating or creeping; salt water.

Family 3 Ciliophryidae Poche

Genus **Ciliophrys** Cienkowski. Spherical with extremely fine

radiating filopodia, giving the appearance of a typical heliozoan, with a single flagellum which is difficult to distinguish from the numerous filopodia, but which becomes conspicuous when the pseudopodia are withdrawn; fresh or salt water.

C. infusionum C. (Fig. 164, *a*). 25–30 μ long; freshwater infusion.

C. marina Caullery. About 10 μ in diameter; salt water.

Family 4 **Lithocollidae** Poche

Genus **Lithocolla** Schulze. Spherical body; outer envelope with usually one layer of sand-grains, diatoms, etc.; nucleus eccentric.

L. globosa S. (Fig. 164, *b*). Body reddish with numerous small colored granules; nucleus large; central granule unknown; envelope 35–50 μ in diameter; in lakes, ponds, and rivers; also in brackish water.

Genus **Astrodisculus** Greeff. Spherical with gelatinous envelope, free from inclusions, sometimes absent; no demarcation between 2 regions of the cytoplasm; pseudopodia fine without granules; fresh water.

A. radians G. (Fig. 164, *c*). Outer surface usually with adherent foreign bodies and bacteria; cytoplasm often loaded with green, yellow, or brown granules; nucleus eccentric; a contractile vacuole; diameter 25–30 μ including envelope; in pools and ditches.

Genus **Actinolophus** Schulze. Body pyriform, enveloped in a gelatinous mantle; stalked; stalk apparently hollow; axopodia long, numerous; nucleus eccentric; salt water.

A. pedunculatus S. (Fig. 164, *d*). Diameter about 30 μ ; stalk about 100 μ long.

Genus **Elaeorhanis** Greeff. Spherical; mucilaginous envelope with sand-grains and diatoms; cytoplasm with a large oil globule; nucleus eccentric; 1 or more contractile vacuoles; pseudopodia not granulated, sometimes forked; fresh water.

E. cincta G. (Fig. 164, *e*). Bluish with a large yellow oil globule; without any food particles; no central granule; pseudopodia rigid, but apparently without axial filaments, sometimes forked; young forms colonial; solitary when mature; outer diameter 50–60 μ ; body itself 25–30 μ ; in lakes and pools.

Genus **Sphaerastrum** Greeff. Somewhat flattened; greater part of axopodia and body covered by a thick gelatinous mantle; a central granule and an eccentric nucleus; fresh water.

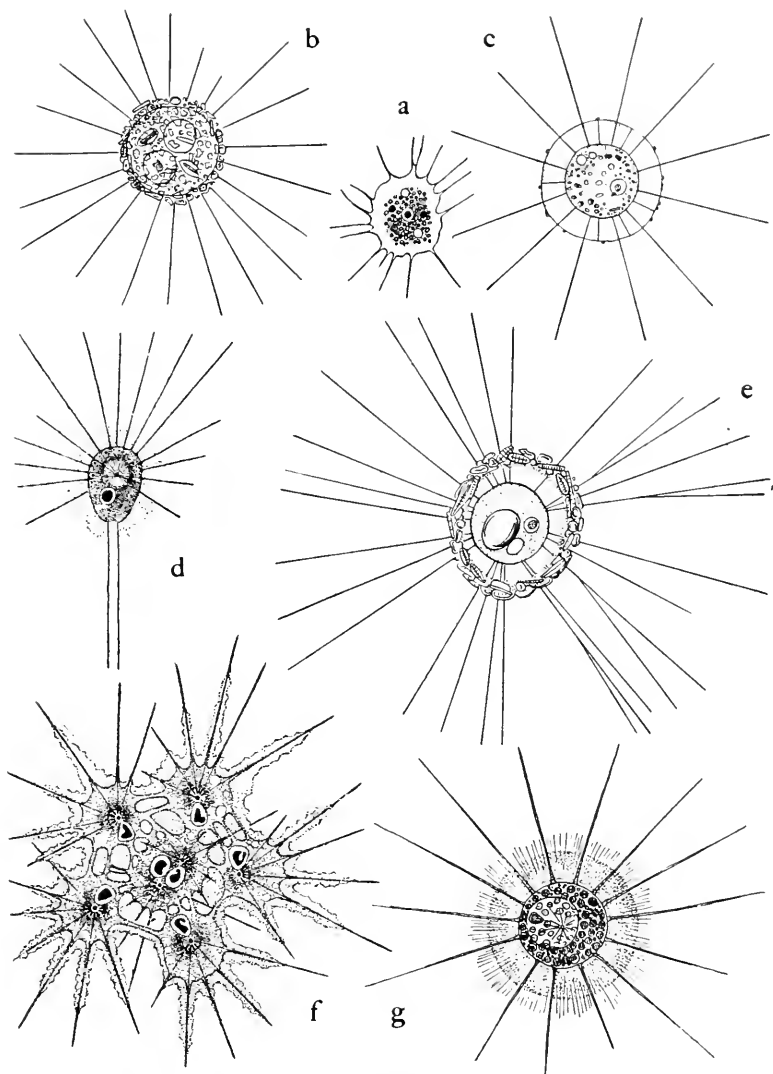


FIG. 164. a, *Ciliophrys infusionum*, $\times 400$ (Bütschli); b, *Lithocolla globosa*, $\times 250$ (Penard); c, *Astrodisculus radians*, $\times 600$ (Penard); d, *Actinolophus pedunculatus*, $\times 400$ (Schultze); e, *Elaeorhans cincta*, $\times 300$ (Penard); f, *Sphaerastrum fockei*, $\times 300$ (Stubenrauch); g, *Heterophrys myriopoda*, $\times 270$ (Penard).

S. fockei G. (Fig. 164, *f*). Diameter about 30μ ; often colonial; in swamps.

Family 5 **Heterophryidae** Poche

Genus **Heterophrys** Archer. Spherical; mucilaginous envelope thick, with numerous radial, chitinous spicules which project beyond periphery; nucleus eccentric; axial filaments originate in a central granule; fresh or salt water.

H. myriopoda A. (Fig. 164, *g*). Nucleus eccentric; cytoplasm loaded with spherical algae, living probably as symbionts; contractile vacuoles indistinct; $50\text{--}80\mu$ in diameter; in pools and marshes; and also among marine algae.

H. glabrescens Penard. Spherical; gelatinous envelope poorly developed; chitinous needles indistinct; pseudopodia very long; $11\text{--}15\mu$ in diameter; fresh water.

Family 6 **Clathrellidae** Poche

Genus **Clathrella** Penard. Envelope distinct, polygonal; surface with uniform alveoli with intervalveolar portion extending out; envelope appears to be continuous, but in reality formed by a series of cup-like bodies; contractile vacuole large; voluminous nucleus eccentric; filopodia straight, rarely bifurcated, arising between "cups."

C. foreli P. (Fig. 165, *a*). Envelope about $40\text{--}55\mu$ in diameter; fresh water.

Family 7 **Acanthocystidae** Claus

Genus **Acanthocystis** Carter. Spherical; siliceous scales, arranged tangentially and radiating siliceous spines with pointed or bifurcated ends; nucleus and endoplasm eccentric; a distinct central granule in which the axial filaments originate. Several species.

A. aculeata Hertwig et Lesser (Fig. 165, *b*). Tangential scales stout and pointed; spines curved and nail-headed; cytoplasm greyish; a single contractile vacuole; diameter $35\text{--}40\mu$; spines about $1/3$ the body diameter; in fresh water.

Genus **Pompholyxophrys** Archer. Spherical; outer mucilaginous envelope with minute colorless spherical granules arranged in concentric layers; nucleus eccentric; contractile vacuoles; pseudopodia long, straight, acicular; fresh water.

P. punicea A. (Fig. 165, *c*). Body colorless or reddish, with

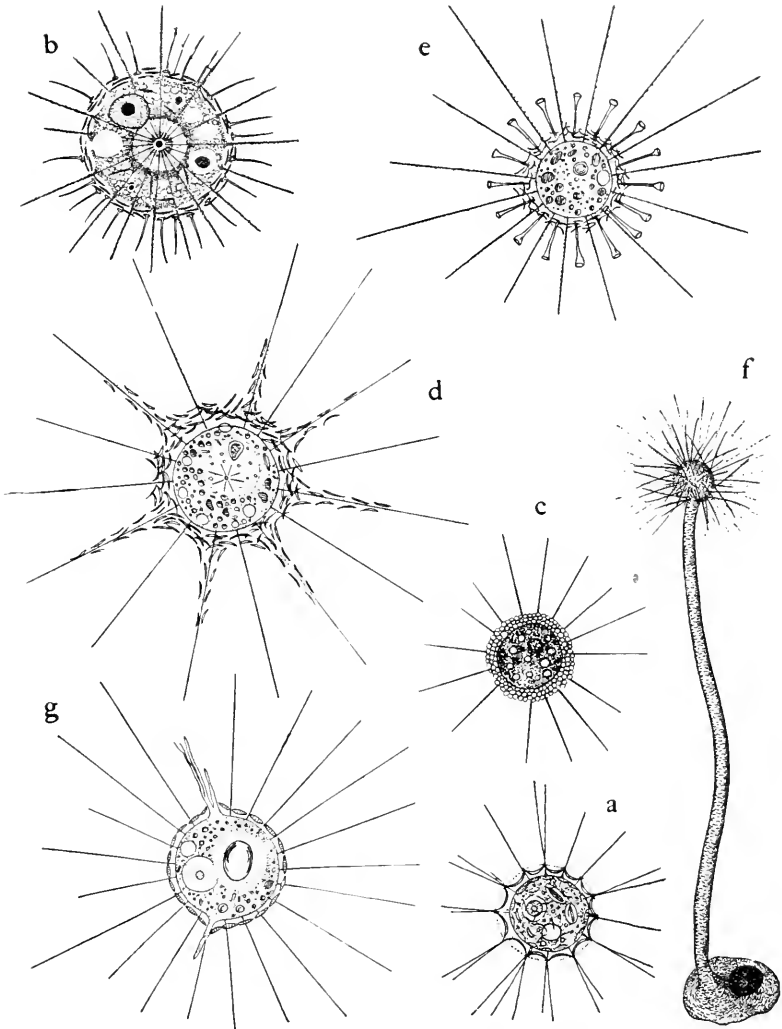


FIG. 165. a, *Clathrella foreli*, $\times 250$ (Penard); b, *Acanthocystis aculeata*, $\times 300$ (Stern); c, *Pompholyxophrys punicea*, $\times 260$ (West); d, *Raphidiophrys pallida*, $\times 300$ (Penard); e, *Raphidocystis tubifera*, $\times 500$ (Penard); f, *Wagnerella borealis*, $\times 75$ (Kühn); g, *Pinaciophora fluvialis*, $\times 250$ (Penard).

usually many colored granules and green or brown food particles; nucleus large, eccentric; solitary, active; diameter $25\text{--}35\mu$; outer envelope $5\text{--}10\mu$ larger; in pools.

Genus **Raphidiophrys** Archer. Spherical; mucilaginous envelope with spindle-shaped or discoidal spicules which extend normally outwards along pseudopodia; nucleus and endoplasm eccentric; solitary or colonial; fresh water. Several species.

R. pallida Schulze (Fig. 165, *d*). Outer gelatinous envelope crowded with curved lenticular spicules, forming accumulations around pseudopodia; ectoplasm granulated; nucleus eccentric; contractile vacuoles; axial filaments arise from the central granule; solitary; diameter $50\text{--}60\mu$; nucleus $12\text{--}15\mu$ in diameter; spicules 20μ long; among vegetation in still fresh water.

Genus **Raphidocystis** Penard. Spicules of various forms, but unlike those found in the last genus.

R. tubifera P. (Fig. 165, *e*). Spicules tubular with enlarged extremity; diameter about 18μ ; envelope 25μ ; fresh water.

Genus **Wagnerella** Mereschkowsky. Spherical, supported by a cylindrical stalk with an enlarged base; small siliceous spicules; nucleus in the base of stalk; multiplication by budding.

W. borealis M. (Fig. 165, *f*). About 180μ in diameter; stalk often up to 1.1 mm. long; salt water.

Genus **Pinaciophora** Greeff. Spherical; outer envelope composed of circular discs, each being perforated with 19 minute pores; cytoplasm reddish; fresh water.

P. fluviatilis G. (Fig. 165, *g*). Diameter $45\text{--}50\mu$, but somewhat variable; in freshwater ponds.

Family 8 Clathrulinidae Claus

Genus **Clathrulina** Cienkowski. Envelope spherical, homogeneous, with numerous regularly arranged openings; with a stalk; protoplasm central, not filling the capsule; nucleus central; pseudopodia numerous, straight or forked, granulated; fresh water.

C. elegans C. (Fig. 166, *a*). Envelope colorless to brown, perforated by numerous comparatively large circular or polygonal openings; 1 or more contractile vacuoles; nucleus central; diameter $60\text{--}90\mu$; openings $6\text{--}10\mu$; stalk 2–4 times the diameter of envelope by $3\text{--}4\mu$ wide; solitary or colonial; among vegetation in ponds.

Genus **Hedriocystis** Hertwig et Lesser. Envelope spherical, openings minute, surrounded by polyhedral facets or ridges; with stalk; solitary or colonial; fresh water.

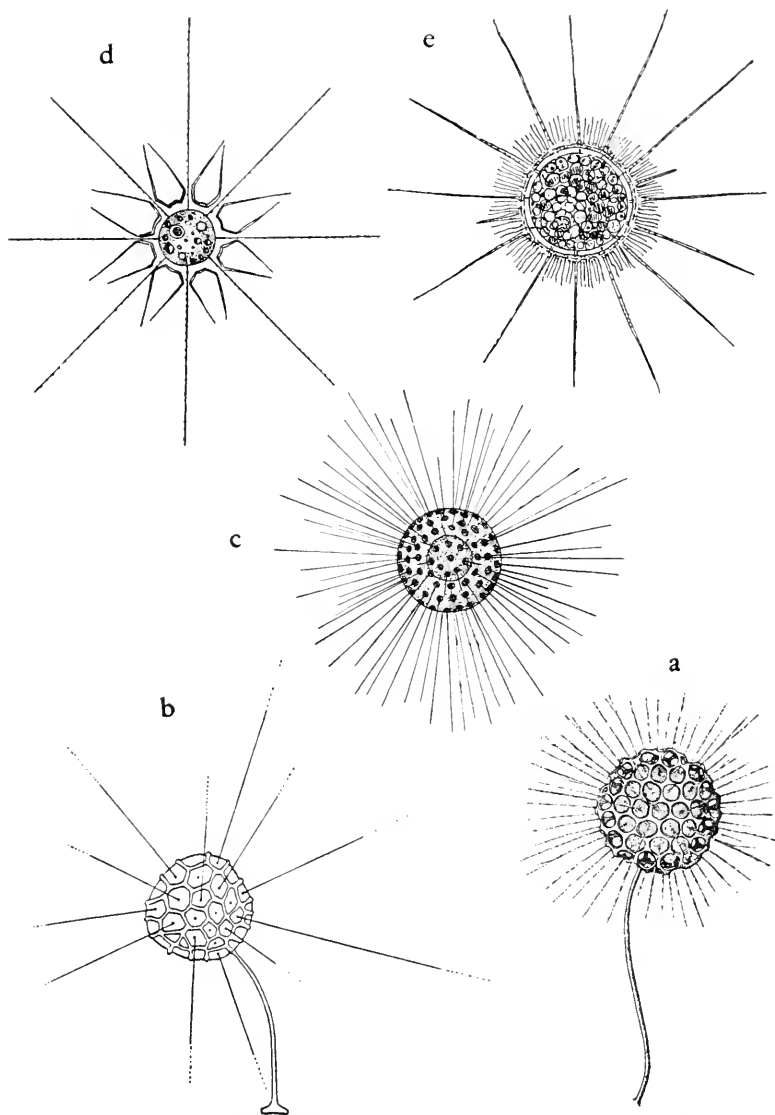


FIG. 166. a, *Clathrulina elegans*, $\times 250$ (Leidy); b, *Hedriocystis reticulata*, $\times 500$ (Brown); c, *Elaster grceffi*, $\times 680$ (Penard); d, *Choanocystis lepidula*, $\times 690$ (Penard); e, *Myriophrys paradoxa*, $\times 300$ (Penard).

H. reticulata Penard (Fig. 166, *b*). Envelope colorless or pale yellow, proliferations regularly polygonal with raised borders; stalk solid, straight; nucleus central; 1 contractile vacuole; each pseudopodium arises from a pore located in the center of a facet; solitary; capsule about 25μ in diameter; body about 12μ in diameter; stalk about 70μ by 1.5μ ; in marshy pools.

Genus **Elaster** Grimm. Envelope spherical, delicate, penetrated by numerous more or less large pores; without stalk; pseudopodia many, straight filopodia.

E. greeffi G. (Fig. 166, *c*). Diameter of envelope 20μ ; envelope delicate, colorless; many pseudopodia; in peaty soil.

Genus **Choanocystis** Penard. Spherical envelope with perforations which possess conical borders; openings of cones provided with funnel-like expansions, edges of which nearly touch one another; fresh water.

C. lepidula P. (Fig. 166, *d*). Diameter $10\text{--}13\mu$; envelope delicate; 1 or more contractile vacuoles; pseudopodia very long.

Family 9 Myriophryidae Poche

Genus **Myriophrys** Penard. Spherical or ovoid, covered with a protoplasmic envelope containing scales(?), surrounded by numerous fine processes; endoplasm vesicular; a large nucleus eccentric; a large contractile vacuole; long pseudopodia granulated and attenuated toward ends.

M. paradoxa P. (Fig. 166, *e*). Average diameter 40μ ; in freshwater swamps.

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CHAPTER 22

Order 2 Radiolaria Müller

THE Radiolaria are pelagic in various oceans. A vast area of the ocean floor is known to be covered with the ooze made up chiefly of radiolarian skeletons. They seem to have been equally abundant during former geologic ages, since rocks composed of their skeletons occur in various geological formations. Thus this group is the second group of Protozoa important to geologists.

The body is generally spherical, although radially or bilaterally symmetrical forms are also encountered. The cytoplasm is divided distinctly into two regions which are sharply delimited by a membranous structure known as the **central capsule**. This is a single or double perforated membrane of pseudochitinous or mucinoid nature. Although its thickness varies a great deal, the capsule is ordinarily very thin and only made visible after addition of reagents. Its shape varies according to the form of the organism; thus in spherical forms it is spherical, in discoidal or lenticular forms it is more or less ellipsoidal, while in a few cases it shows a number of protruding processes. The capsule is capable of extension as the organism grows and of dissolution at the time of multiplication. The cytoplasm on either side of the capsule communicates with the other side through pores which may be large and few or small and numerous. The intracapsular portion of the body is the seat of reproduction, while the extracapsular region is nutritive and hydrostatic in function. The intracapsular cytoplasm is granulated, often greatly vacuolated, and is stratified either radially or concentrically. It contains one or more nuclei, pigments, oil droplets, fat globules, and crystals. The nucleus is usually of vesicular type, but its form, size, and structure, vary among different species and also at different stages of development even in one and the same species.

A thin assimilative layer, or matrix, surrounds the central capsule. In Tripylea, waste material forms a brownish mass known as phaeodium, around the chief aperture (astropyle) of the capsule. Then there is a highly alveolated region, termed calymma, in which the alveoli are apparently filled with a mucilaginous secretion of the cytoplasm. Brandt showed that the

vertical movement of some Radiolaria is due to the formation and expulsion of a fluid which consists of water saturated with carbon dioxide. Under ordinary weather and temperature conditions, the interchange between the alveoli and the exterior is gradual and there is a balance of loss and gain of the fluid, so that the organisms float on the surface of the sea. Under rough weather conditions or at extraordinary high temperatures, the pseudopodia are withdrawn, the alveoli burst, and the organisms descend into deeper water, where the alveoli are reformed.

The Radiolaria feed on microplankton such as copepods, diatoms, and various Protozoa. The food is taken in through pseudopodia and passed down into the deeper region of calymma where it is digested in food vacuoles. The Radiolaria can, however, live under experimental conditions without solid food if kept under light. This is ordinarily attributed to the action of the yellow corpuscles which are present in various parts of the body, although they are, as a rule, located in the calymma. In Actipylea they are found only in intracapsular cytoplasm, and in Tripylea they are absent altogether. They are spherical bodies, about 15μ in diameter, with a cellulose wall, 2 chromatophores, a pyrenoid, starch, and a single nucleus. They appear to multiply by fission. These bodies are considered as zooxanthellae (p. 23-24). In the absence of organic food material, the Radiolaria live probably by utilizing the products of holophytic nutrition of these symbiotic organisms.

The axopodia arise from either the extracapsular or the intracapsular portion and radiate in spherical forms in all directions, as in Heliozoa. In Actipylea, myonemes are present in certain pseudopodia and produce circular groups of short, rod-like bodies, clustered around each of the radial spines (Fig. 168, *c*). They connect the peripheral portion of the body with the pseudopodial covering of the spicule and possess a great contractile power, supposedly with hydrostatic function (p. 52-53).

The skeletal structure of Radiolaria varies considerably from simple to complex and has a taxonomic value. The chemical nature of the skeleton is used in distinguishing the major subdivisions of the order. In the Actipylea it seems to be made up of strontium sulphate, while in the three other groups, Peripylea, Monopylea, and Tripylea, it consists fundamentally of siliceous substances. The skeleton of the Actipylea is sharply marked

from others in form and structure. The majority of this group possess 20 rods radiating from the center. The rod-shaped skeletons emerge from the body in most cases along five circles, which are comparable to the equatorial, two tropical and two circum-polar circles of the globe, which arrangement is known as Müller's law, since J. Müller first noticed it in 1858.

The life-cycle of the Radiolaria is very incompletely known (Fig. 167). Binary or multiple fission or budding has been seen in some Peripylea, Actipylea, and Tripylea. Multiple division is

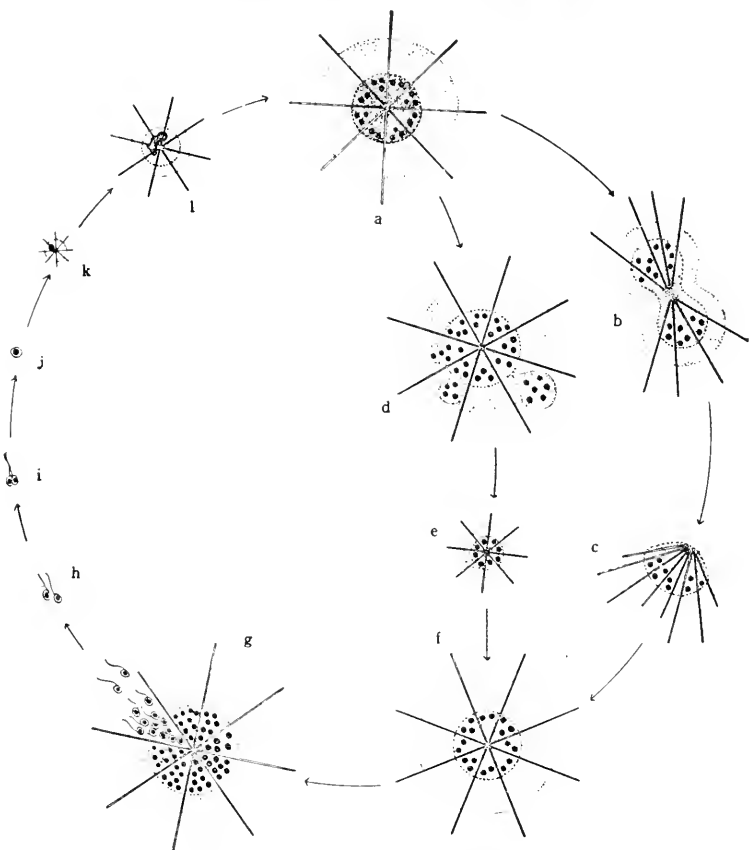


FIG. 167. Diagram illustrating the life-cycle of *Actipylea* (Kühn). a, mature individual; b, c, binary fission; d, e, multiplication by budding; f, mature individual similar to a; g, formation of swarmers; h-j, supposed, but not observed, gametogony of two swarmers producing a zygote; k, l, young individuals.

also known to occur in Thalassophysidae in which it is the sole known means of reproduction. The central capsule becomes very irregular in its outline and the nucleus breaks up into numerous chromatin globules. Finally the capsule and the intracapsular cytoplasm become transformed into numerous small bodies, each containing several nuclei. Further changes are unknown. Swarmer-formation is known in some forms. In *Thalassicolla*, the central capsule becomes separated from the remaining part of the body and the nuclei divide into a number of small nuclei, around each of which condenses a small ovoidal mass of cytoplasm. They soon develop flagella. In the meantime the capsule descends to a depth of several hundred meters, where its wall bursts and the flagellate swimmers are liberated (*g*). Both isoswarmers and anisoswarmers occur. The former often contain a crystal and a few fat globules. Of the latter, the macroswarmers possess a nucleus and refringent spherules in the cytoplasm only. Some forms possess 2 flagella, one of which is coiled around the groove of the body, which makes them resemble certain dinoflagellates. Further development is unknown; it is supposed that the anisoswarmers are sexual and isoswarmers asexual generations.

Enormous numbers of species of Radiolaria are known. An outline of the classification is given below, together with a few examples of the genera.

- Skeleton composed of strontium sulphate.....
-Suborder 1 Actipylea
- Skeleton composed of other substances
- Central capsule uniformly perforated; skeleton either tangential to the capsule or radiating without reaching the intracapsular region.....Suborder 2 Peripylea (p. 372)
- Central capsule not uniformly perforated
- Capsule monaxonic, bears at one pole a perforated plate forming the base of an inward-directed cone.....
-Suborder 3 Monopylea (p. 373)
- Capsule with 3 openings: 1 astropyle and 2 parapyles.....
-Suborder 4 Tripylea (p. 374)

Suborder 1 Actipylea Hertwig

- Radial spines, 10–200, not arranged according to Müller's law.....
-Legion 1 Actinelida
- Spines radiate from a common center; ancestral forms (Haeckel)...
-Family 1 Actineliidae

Genus **Actinelius** (Fig. 168, *a*)

10–16 spines irregularly set..... Family 2 Acanthociasmidae

Genus **Acanthociasma** (Fig. 168, *b*)

Radial spines, few, arranged according to Müller's law

Without tangential skeletons..... Legion 2 Acanthometrida

Spines more or less uniform in size

Spicules circular in cross-section... Family 1 Acanthometridae

Genus **Acanthometron** (Fig. 168, *c*)

Spicules cruciform in cross-section.... Family 2 Acanthoniidae

Genus **Acanthonia** (Fig. 168, *d*)

2 opposite spines much larger..... Family 3 Amphilonchidae

Genus **Amphilonche** (Fig. 168, *e*)

With tangential skeletons..... Legion 3 Acanthophractida

20 radial spines of equal size; shell composed of small plates, each with one pore..... Family 1 Sphaerocapsidae

Genus **Sphaerocapsa**

2 or 6 larger spines

2 enormously large conical sheathed spines.....

..... Family 2 Diploconidae

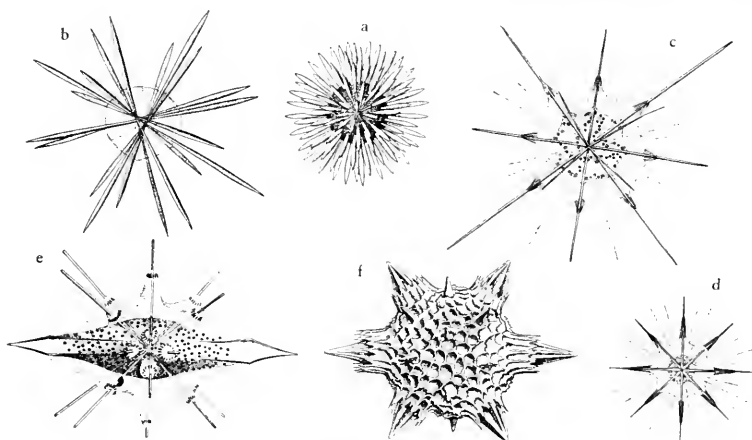


FIG. 168. *a*, *Actinelius primordialis*, $\times 25$ (Haeckel); *b*, *Acanthociasma planum*, $\times 65$ (Mielck); *c*, *Acanthometron elasticum* (Hertwig); *d*, *Acanthonia tetracopa*, $\times 40$ (Schewiakoff); *e*, *Amphilonche hydro-metrica*, $\times 130$ (Haeckel); *f*, *Hexaconus serratus*, $\times 100$ (Haeckel). (From Kühn.)

Genus **Diploconus**

6 large spines.....Family 3 Hexalaspidae

Genus **Hexaconus** (Fig. 168, f)Suborder 2 **Peripylea** Hertwig

Solitary; skeleton wanting or simple spicules; mostly spherical.....

.....Legion 1 Collodaria

Nucleus spherical with smooth membrane

Vacuoles intracapsular.....Family 1 Physematiidae

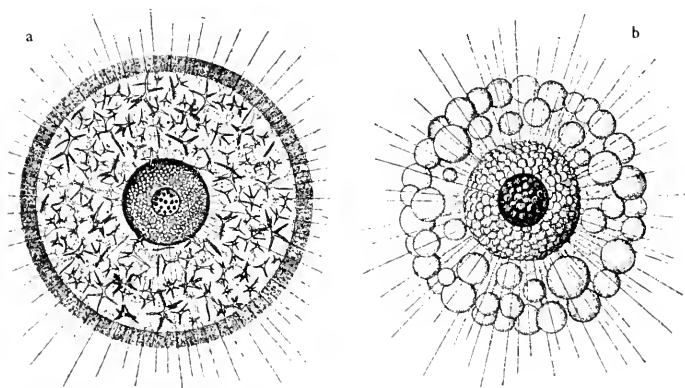
Genus **Lampoxanthium** (Fig. 169, a)

Vacuoles extracapsular.....Family 2 Thalassicollidae

Genus **Thalassicolla** (Fig. 169, b)

Nuclear membrane not smoothly contoured

Nuclear wall branching out into pouches; structure similar to the last.....Family 3 Thalassophysidae

Genus **Thalassophysa**FIG. 169. a, *Lampoxanthium pandora*, $\times 20$ (Haeckel); b, *Thalassicolla nucleata*, $\times 15$ (Huth). (From Kühn.)

Nuclear wall crenate

Huge double spicule.....Family 4 Thalassothamnidae

Genus **Thalassothamnus**

A latticed skeleton, with branching and thorny spines.....

.....Family 5 Orosphaeridae

Genus **Orosphaera**

Solitary; skeleton complex, often concentric....Legion 2 Sphaerellaria

Central capsule and skeleton spherical.....Family 1 Sphaeroidae

Genus **Hexacontium** (Fig. 170, *a*)

Central capsule and skeleton elliptical or cylindrical.....
.....Family 2 Prunoidae

Genus **Pipetta** (Fig. 170, *b*)

Central capsule and skeleton discoidal or lenticular.....
.....Family 3 Discoidae

Genus **Staurocyelia** (Fig. 170, *c*)

Similar to the above, but flattened.....Family 4 Larcoidae

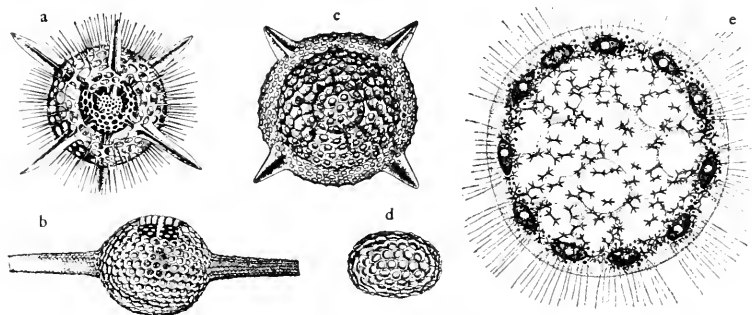


FIG. 170. *a*, *Hexacontium asteracanthion*, $\times 130$; *b*, *Pipetta tuba*, $\times 100$; *c*, *Staurocyelia phacostaurus*, $\times 130$; *d*, *Cenolarius primordialis*, $\times 100$; *e*, *Sphaerozoum ovodimare*, $\times 30$ (Haeckel from Kühn).

Genus **Cenolarius** (Fig. 170, *d*)

Colonial; individuals with anastomosing extracapsular cytoplasm, embedded in a jelly mass.....Legion 3 Polycyttaria
Without latticed skeleton, but with siliceous spicules arranged tangentially to central capsule.....Family 1 Sphaerozoidae

Genus **Sphaerozoum** (Fig. 170, *e*)

Central capsule of each individual enclosed in a latticed skeleton..
.....Family 2 Collosphaeridae

Genus **Collosphaera**Suborder 3 **Monopylea** Hertwig

Without any skeleton.....Legion 1 Nassoidae
.....Family 1 Nassoidae

Genus **Cystidium** (Fig. 171, *a*)

With skeleton

Without a complete latticed skeleton.....Legion 2 Plectellaria
Skeleton a basal tripod.....Family 1 Plectoidae

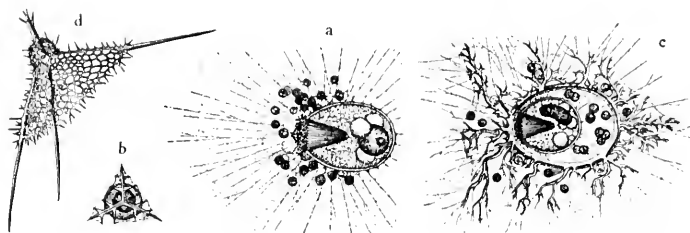
Genus **Triplagia** (Fig. 171, b)

FIG. 171. a, *Cystidium princeps*, $\times 120$; b, *Triplagia primordialis*, $\times 25$; c, *Lithocircus magnificus*, $\times 100$; d, *Dictyophimus hertwigi*, $\times 80$ (Haeckel from Kühn).

Skeleton a simple or multiple sagittal ring.....
.....Family 2 Stephoidae

Genus **Lithocircus** (Fig. 171, c)

With a complete latticed skeleton.....Legion 3 Cyrtellaria
Lattice skeleton single, without constriction.....
.....Family 1 Cyrtoidae

Genus **Dictyophimus** (Fig. 171, d)

Lattice skeleton multiple.....Family 2 Botryoidae

Genus **Phormobothrys**Suborder 4 **Triplylea** Hertwig

Without skeleton; with isolated spicules....Legion 1 Phaeocystina
Skeleton consists of radial hollow rods and fine tangential needles
.....Family 1 Aulacanthidae

Genus **Aulacantha** (Fig. 172, a)

With foreign skeleton covering body surface.....
.....Family 2 Caementellidae

Genus **Caementella** (Fig. 172, b)

With skeleton
1-2 (concentric) usually spherical skeletons.....
.....Legion 2 Phaeosphaeria
Outer lattice skeleton with triangular or areolar meshes.....
.....Family 1 Sagosphaeridae

Genus **Sagenoscene**

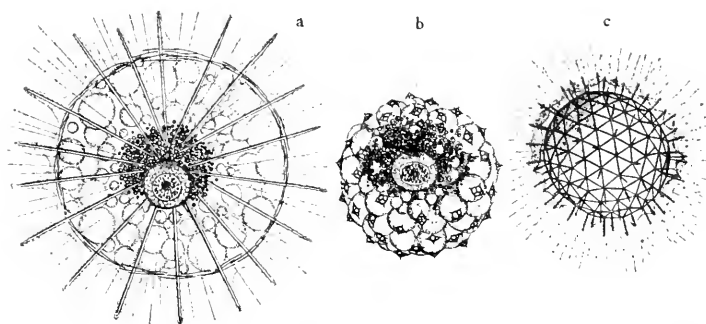


FIG. 172. a, *Aulacantha scolymantha*, $\times 30$ (Kühn); b, *Caementella stupedia*, $\times 65$ (Haeckel); c, *Aulosphaera labradoriensis*, $\times 10$ (Haecker). (From Kühn.)

One lattice skeleton with hollow radial bars.....
..... Family 2 Aulosphaeridae

Genus **Aulosphaera** (Fig. 172, c)

2 concentric lattice skeletons connected by radial bars.....
..... Family 3 Cannosphaeridae

Genus **Cannosphaera**

One skeleton, simple, but variable in shape, bilaterally symmetrical
..... Legion 3 Phaeogromia
Skeleton with fine diatomaceous graining.....
..... Family 1 Challengeridae

Genus **Challengeron** (Fig. 173, a)

Skeleton smooth or with small spines.... Family 2 Medusettidae

Genus **Medusetta** (Fig. 173, b)

One skeleton; spherical or polyhedral, with an opening and with
radiating spines..... Legion 4 Phaeocalpia
Skeleton spherical or polyhedral, with uniformly large round pores
..... Family 1 Castanellidae

Genus **Castanidium** (Fig. 173, c)

Skeleton similar to the last, but the base of each radial spine
surrounded by pores..... Family 2 Circoporidae

Genus **Circoporus** (Fig. 173, d)

Skeleton flask-shaped with 1-2 groups of spines.....
..... Family 3 Tuscaroridae

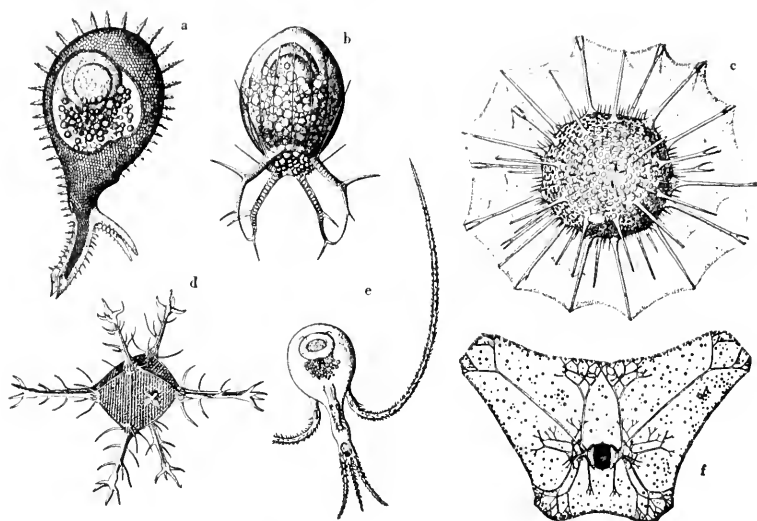


FIG. 173. a, *Challengeron wyvillei*, $\times 105$ (Haeckel); b, *Medusetta ansata*, $\times 230$ (Borgert); c, *Castanidium murrayi*, $\times 25$ (Haeckel); d, *Circoporus octahedrus*, $\times 65$ (Haeckel); e, *Tuscarora murrayi*, $\times 7$ (Haeckel); f, *Coelodendrum ramosissimum*, $\times 10$ (Haeckel). (From Kühn.)

Genus *Tuscarora* (Fig. 173, e)

Central portion of skeleton consists of 2 valves.....

..... Legion 5 Phaeoconchia

Valves thin, each with a conical process which divides into
branched tubes..... Family 1 Coelodendridae

Genus *Coelodendrum* (Fig. 173, f)

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Class 3 Sporozoa Leuckart

THE Sporozoa are without exception parasitic and bear spores in their development. Their hosts are distributed in every animal phylum, from Protozoa to Chordata. As a rule, they are incapable of locomotion, but some when immature may move about by means of pseudopodia. They possess neither cilia nor flagella, except as gametes. In the forms that are confined to one host, the spore usually is enveloped by a resistant membrane which would enable it to withstand unfavorable conditions while outside of the host body, but in those having two host animals, as in *Plasmodium*, the sporozoite is naked. The method of nutrition is saprozoic or parasitic, the food being dissolved cytoplasm, tissue fluid, body fluid, or dissolved food material of the host.

Both asexual and sexual reproductions are well known in many species. Asexual reproduction by repeated binary or multiple fission or budding of intracellular trophozoites or **schizonts**, produces far greater number of individuals than that of protozoans belonging to other classes and often is referred to as **schizogony**. The sexual reproduction is by isogamous or anisogamous fusion or autogamy and marks in many cases the beginning of **sporogony** or spore-formation, the initial stage being the zygote or **sporont**.

Schaudinn divided the Sporozoa into two groups, Telosporidia and Neosporidia, and this scheme has been followed by several authors. Some recent writers consider these two groups as separate classes. This, however, seems to be improper, as the basis of distinction between them is entirely different from that which is used for distinguishing the other four classes: Sarcodina, Mastigophora, Ciliata, and Suctoria. For this reason, the Sporozoa are placed in a single class and divided into three subclasses as follows:

Spore simple; without polar filament

Spore with or without membrane; with 1-many sporozoites.....
.....Subclass 1 Telosporidia (p. 378)

Spore with membrane; with one sporozoite..... Subclass 2 Acnidosporidia (p. 446)

Spore with polar filament.....Subclass 3 Cnidosporidia (p. 453)

Subclass 1 **Telosporidia** Schaudinn

The spore which contains neither a polar capsule nor a polar filament, possesses one to several sporozoites and is formed at the end of the trophic life of the individual. In the forms which invade two host animals to complete their development, there occur naked sporozoites instead of spores.

The infection of a new host begins with the entrance of mature spores through mouth, or with the introduction of the sporozoites by blood-sucking invertebrates directly into the blood stream. The sporozoites enter specific host cells and there grow at the expense of the latter. In the Coccidia and the Haemosporidia the schizont continues its intracellular existence, but in the Gregarinida it leaves the host cell and grows in an organ cavity. Except Eugregarinina, the vegetative form undergoes schizogony and produces a large number of schizonts which invade new host cells, thus spreading the infection within the host body. The schizonts finally develop into gametocytes. In the Coccidia and the Haemosporidia, anisogametes are, as a rule, produced. Each macrogametocyte develops into a single macrogamete and each microgametocyte, into several microgametes. Fusion of two gametes results in formation of a large number of zygotes, each of which develops either into one to many spores or into a number of naked sporozoites. In the Gregarinida, two fully mature trophozoites (or gametocytes) encyst together and the nucleus in each multiplies repeatedly to form numerous gametes, which fuse in pairs with those produced in the other individual within the common envelope. The zygotes develop into spores, each containing sporozoites of variable number. When these spores enter a new host, the changes outlined above are repeated. The Telosporidia are parasitic in vertebrates and higher invertebrates.

Three orders are distinguished in this subclass:

- Mature trophozoite extracellular, large; zygote not motile; sporozoites enveloped.....Order 1 Gregarinida
 Mature trophozoite intracellular, small
 Zygote not motile; sporozoites enveloped. Order 2 Coccidia (p. 415)
 Zygote motile; sporozoites naked..Order 3 Haemosporidia (p. 434)

Order 1 **Gregarinida** Lankester

The gregarines are chiefly coelozoic parasites in invertebrates, especially arthropods and annelids. They obtain their nourish-

ment from the host organ-cavity through osmosis. The vast majority of gregarines do not undergo schizogony and increase in number is carried on solely by sporogony. In a small group, however, schizogony takes place as well as sexual reproduction and this is used as the basis for grouping these protozoans into two suborders as follows:

No schizogony.....Suborder 1 Eugregarinina
Schizogony occurs.....Suborder 2 Schizogregarinaria (p. 409)

Suborder 1 **Eugregarinina** Doflein

This suborder includes the majority of the so-called gregarines which are common parasites of arthropods. When the spore gains entrance to a suitable host, it germinates and the sporozoites emerge and enter the epithelial cells of the digestive tract. There they grow at the expense of the host cells which they leave soon and to which they become attached by various organellae of attachment (Fig. 174). These trophozoites become detached from

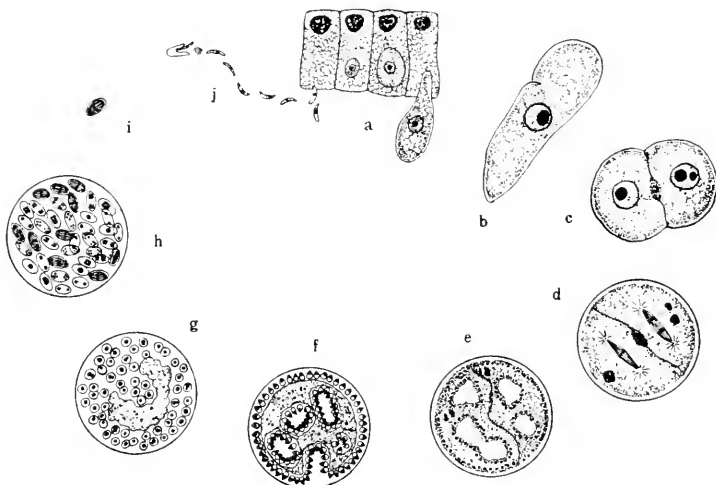


FIG. 174. The life-cycle of *Lankesteria culicis*, \times about 500 (Wenyon). a, entrance of sporozoites into the epithelial cell and growth stages of trophozoites; b, mature trophozoite; c, association of two trophozoites; d-f, gamete-formation; g, gametogony; h, development of spores from zygotes; i, a spore; j, germination of spore in host gut.

the host cells and move about in the lumen of the gut. This stage, **sporadin**, is ordinarily most frequently recognized. It is usually large and vermiform. The body is covered by a definite pellicle

and its cytoplasm is clearly differentiated into the ectoplasm and endoplasm. The former contains myonemes (p. 52) which enable the organisms to undergo gliding movements. In one group, Acephalina, the body is of a single compartment, but in the other group, Cephalina, the body is divided into two compartments by an ectoplasmic septum. The smaller anterior part is the **protomerite** and the larger posterior part, the **deutomerite**, contains a single nucleus except in *Pileocephalus* (p. 404) in which the nucleus is said to be located in the protomerite. The endoplasm contains numerous spherical or ovoidal bodies which are called zooamylum or paraglycogen grains and which are apparently reserve food material (p. 94). The protomerite may possess an attaching process with hooks or other structures at its anterior border, which is called the **epimerite**. The epimerite is usually not found on detached sporadins. Trophozoite with the epimerite will be called the **cephalin**. Many gregarines are solitary, while others are found often in an endwise association of two or more sporadins. This association is called **syzygy**. The anterior individual is known as the **primit** and the posterior, the **satellite**. Sporadins usually encyst in pairs and become gametocytes. Within the cyst-membrane, the nucleus in each individual undergoes repeated division, forming a large number of small nuclei which by a process of budding transform themselves into numerous gametes. The gametes may be isogamous or anisogamous. Each of the gametes in one gametocyte appears to unite with one formed in the other, so that a large number of zygotes are produced. The zygote becomes surrounded by a resistant membrane and its contents develop into the sporozoites, thus developing into a spore. The spores germinate when taken into the alimentary canal of a host animal and the life-cycle is repeated.

According to Wenyon, in a typical Eugregarinina, *Lankesteria culicis* (Fig. 174) of *Aedes aegypti*, the development in a new host begins when the latter ingests the spores which had been set free by infected adult mosquitoes in the water. From each spore are liberated 8 sporozoites (*j*), which enter the epithelial cells of the stomach and grow (*a*). These vegetative forms leave the host cells later and become mingled with the food material present in the stomach lumen of the host (*b*). When the larva pupates, the sporadins enter the Malpighian tubules, where they encyst (*c*).

The repeated nuclear division is followed by formation of large numbers of gametes (*d-f*) which unite in pairs (*g*). The zygotes thus formed develop into spores, each possessing 8 sporozoites (*h*). Meanwhile the host pupa emerges as an adult mosquito, and the spores which become set free in the lumen of the tubules, pass into the intestine, from which they are discharged into water. Larvae swallow the spores and acquire infection.

Eugregarinina are divided into 2 tribes:

Trophozoite not septate.....Tribe 1 Acephalina
Trophozoite septate.....Tribe 2 Cephalina (p. 391)

Tribe 1 **Acephalina** K  lliker

The acephalines are mainly found in the body cavity and organs associated with it. The infection begins by the ingestion of mature spores by a host, in the digestive tract of which the sporozoites are set free and undergo development or make their way through the gut wall and reach the coelom or various organs such as seminal vesicles. Young trophozoites are intracellular, while more mature forms are either intracellular or extracellular.

Spores with similar extremities

Spores biconical

Sporadins solitary

Anterior end not differentiated.....

.....Family 1 Monocystidae (p. 382)

Anterior end with a conical or cylindro-conical trunk.....

.....Family 2 Rhynchocystidae (p. 384)

Sporadins in syzygy

Spores with thickenings at ends.....

.....Family 3 Zygoecystidae (p. 384)

Spores without thickenings.....

.....Family 4 Aikinetocystidae (p. 385)

Spores not biconical

Spores navicular.....Family 5 Stomatophoridae (p. 386)

Spores round or oval

No encystment.....Family 6 Schaudinnellidae (p. 387)

2 sporadins encyst together...Family 7 Diplocystidae (p. 387)

Spores with dissimilar ends

Spores with epispore.....Family 8 Urosporidae (p. 389)

Spores without epispore.....Family 9 Allantocystidae (p. 391)

Spores unobserved; grown trophozoites with cup-like depression at posterior end to effect syzygy.....

.....Family 10 Ganymedidae (p. 391)

Family 1 **Monocystidae** Bütschli

Trophozoites spheroidal to cylindrical; anterior end not differentiated; solitary; spores biconical, without any spines, with 8 sporozoites.

Genus **Monocystis** Stein. Trophozoites variable in form; motile; incomplete sporulation in cyst; spore biconical, symmetrical; in coelom or seminal vesicles of oligochaetes. Numerous species.

M. ventrosa Berlin (Fig. 175, *a-c*). Sporadins $109-183\mu$ by $72-135\mu$; nucleus up to 43μ by 20μ ; cysts $185-223\mu$ by $154-182\mu$; spores $17-25\mu$ by $8-10\mu$; in *Lumbricus rubellus*, *L. castaneus* and *Eisenia foetida*.

M. lumbrici Henle (Fig. 175, *d, e*). Sporadins about 200μ by $60-70\mu$; cysts about 162μ in diameter; in *Lumbricus terrestris*, *L. rubellus*, and *L. castaneus*.

Genus **Apolocystis** Cognetti. Trophozoites spherical; without principal axis marked by presence of any special peripheral organ; solitary; spore biconical; in seminal vesicles or coelom of various oligochaetes. Many species.

A. gigantea Troisi (Fig. 175, *f*). In seminal vesicles of *Helodrilus foetidus* and *Lumbricus rubellus*; late October to March only; fully grown trophozoites $250-800\mu$ in diameter; whitish to naked eyes; pellicle thickly covered by $10-15\mu$ long 'hairs'; endoplasm packed with spherical paraglycogen grains (3μ in diameter); nucleus $35-43\mu$ in diameter; cysts $400-800\mu$ in diameter; spores 19μ by 8.6μ .

A. minuta Troisi (Fig. 175, *g*). In seminal vesicles of *Lumbricus terrestris*, *L. castaneus* and *L. rubellus*; mature trophozoites $40-46\mu$ in diameter; endoplasm yellowish brown, packed with spherical paraglycogen grains ($5.3-7\mu$ in diameter); nucleus 10μ in diameter; cysts $68-74\mu$ by $55-65\mu$; spores of 3 sizes, 11μ by 5.5μ , 18.8μ by 7μ and 21.6μ by 9.8μ .

Genus **Nematocystis** Hesse. Trophozoites elongate, cylindrical and shaped like a nematode; solitary. Many species.

N. vermicularis H. (Fig. 175, *h*). In seminal vesicles of *Lumbricus terrestris*, *L. rubellus*, *Helodrilus longus*, *Pheretima barbadensis*; trophozoites 1 mm. by 100μ ; cylindrical, both ends with projections; nucleus oval; endoplasm alveolated, with paraglycogen grains; sporadins become paired lengthwise; cysts and spores unknown.

Genus **Rhabdocystis** Boldt. Trophozoites elongate, gently

curved; anterior end swollen, club-shaped; posterior end attenuated; spores with sharply pointed ends. One species.

R. claviformis B. (Fig. 175, i, j). In seminal vesicles of *Octo-*

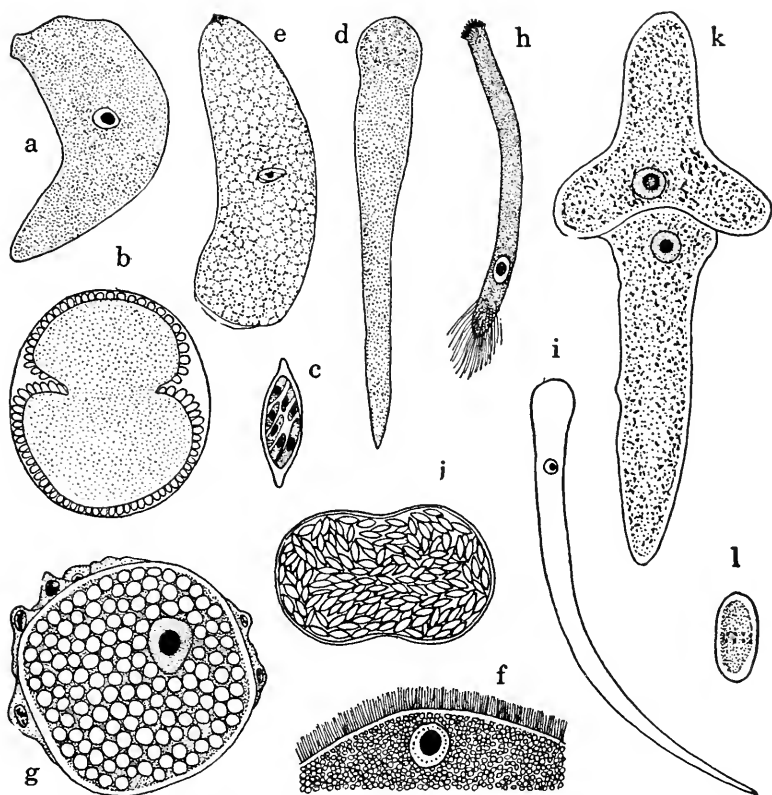


FIG. 175. a-c, *Monocystis ventrosa* (a, $\times 260$; b, $\times 150$; c, $\times 830$) (Berlin); d, e, *M. lumbrici*, $\times 280$ (Berlin); f, *Apolocystis gigantea*, $\times 90$ (Troisi); g, *A. minuta*, with attached phagocytes, $\times 770$ (Troisi); h, *Nematocystis vermicularis*, $\times 80$ (Hesse); i, j, *Rhabdocystis claviformis* (i, $\times 220$; j, $\times 270$) (Boldt); k, l, *Enterocystis ensis* (k, $\times 140$) (Zwetkow).

lasium complanatum; sporadins extended, up to 300μ by 30μ ; pellicle distinctly longitudinally striated; zooamylum bodies $2-4\mu$ in diameter; cysts biscuit-form, 110μ by 70μ ; spores 16μ by 8μ .

Genus **Enterocystis** Zwetkow. Early stages of trophozoites in syzygy; sporadins in association ensiform; cysts spherical without

ducts; spores elongate ovoid, with 8 sporozoites; in gut of ephemeropterid larvae.

E. ensis Z. (Fig. 175, *k, l*). Sporadins in syzygy 200–510 μ long; cysts 200–350 μ in diameter; spores elongate ovoid; in gut of larvae of *Caenis* sp.

Family 2 Rhynchocystidae Bhatia

Trophozoites ovoid, spherical or elongate, with a conical or cylindro-conical trunk at anterior end; solitary; spore biconical, with 8 sporozoites.

Genus **Rhynchocystis** Hesse. Trophozoites ovoid or cylindrical; plastic epimerite, conical or cylindro-conical trunk; in seminal vesicles of oligochaetes. Many species.

R. pilosa Cuénot (Fig. 176, *a*). In seminal vesicles of *Lumbricus terrestris*, *L. castaneus* and *Helodrilus foetidus*; 217 μ by 25.5 μ ; pellicle with close, longitudinal ridges from which arise 'hairs' up to 40 μ in length; endoplasm viscous, packed with oval (3 μ by 2 μ) zooamylum bodies; cysts ovoid, 95 μ by 84 μ ; spores 13.3 μ by 5 μ .

R. porrecta Schmidt (Fig. 176, *b, c*). In seminal vesicles of *Lumbricus rubellus* and *Helodrilus foetidus*; extremely long with an enlarged head; up to 2.5 mm. by 32–36 μ ; sluggish; endoplasm granulated, filled with oval (4 μ by 2–3 μ) paraglycogen grains; nucleus 17–25 μ in diameter; spores 27.7–28 μ by 12 μ ; sporozoites 13–18 μ by 3–5 μ .

Family 3 Zygcystidae Bhatia

Trophozoites in association, spores biconical, with peculiar thickenings at extremities; with 8 sporozoites; in seminal vesicles or coelom of oligochaetes.

Genus **Zygcystis** Stein. Sporadins pyriform, 2–3 in syzygy; in seminal vesicles or coelom of oligochaetes. Several species.

Z. wenrichi Troisi (Fig. 176, *d, e*). In seminal vesicles of *Lumbricus rubellus* and *Helodrilus foetidus*; sporadins up to 1.5 mm. by 250 μ in diameter; pellicle with longitudinal ridges which become free and form a 'tuft of hairs' at the posterior end; cysts 500–800 μ by 300–500 μ ; spores 28 μ by 13 μ .

Genus **Pleurocystis** Hesse. Trophozoites in longitudinal or lateral association; spores biconical. One species.

P. cuenoti H. (Fig. 176, *f*). In the ciliated seminal horn of *Helodrilus longus* and *H. caliginosus*; 2 mm. by 300 μ ; pellicle

striated longitudinally, oblique near the posterior end; cysts 1.5–2 mm. in diameter; spores 28.5μ by 12μ .

Family 4 Aikinetocystidae Bhatia

Trophozoites solitary or in syzygy; branching dichotomously, branches with sucker-like organellae of attachment; spores biconical.

Genus **Aikinetocystis** Gates. Trophozoites cylindrical or columnar, with a characteristic, regular dichotomous branching at attached end, with sucker-like bodies borne on ultimate branches; solitary or 2 (3–8) individuals in association; spores biconical.

A. singularis G. (Fig. 176, *g, h*). In coelom of *Eutyphoeus foveatus*, *E. rarus*, *E. peguanus* and *E. spinulosus* (Burma); trophozoites up to 4 mm. long; number of branches 8 or 16, each with an irregular sucker; ovoid nucleus near rounded end; spores of two sizes, 20–23 μ long and 7–8 μ long; a few cysts found, ovoid and 620 μ long.

Family 5 Stomatophoridae Bhatia

Trophozoites spherical to cylindrical or cup-shaped; with a sucker-like epimerite; solitary; spores navicular, ends truncate; 8 sporozoites; in seminal vesicles of *Pheretima* (Oligochaeta).

Genus **Stomatophora** Drzewiecki. Trophozoites spherical or ovoid; anterior end with a sucker-like epimeritic organella with a central mucron; spores navicular. Several species.

S. coronata (Hesse) (Fig. 176, *i–k*). In seminal vesicles of *Pheretima rodericensis*, *P. hawayana* and *P. barbadensis*; trophozoites spherical, ovoid or elliptical, about 180 μ by 130 μ ; endoplasm with ovoid zooamylum grains; cysts ellipsoid or fusiform, 70–80 μ by 50–60 μ ; spores in 2 sizes, 11 μ by 6 μ and 7 μ by 3 μ and in chain.

Genus **Astrocystella** Cognetti. Trophozoites solitary; stellate with 5–9 lobes radiating from central part containing nucleus; anterior surface with a depression. One species.

A. lobosa C. (Fig. 176, *l*). In seminal vesicles of *Pheretima beaufortii* (New Guinea); diameter about 200 μ ; spores fusiform.

Genus **Craterocystis** Cognetti. Trophozoites solitary; rounded; a sucker-like depression on anterior end; myonemes well developed, running from concave to convex side. One species.

C. papua C. (Fig. 176, *m*). In prostate and lymphatic glands of

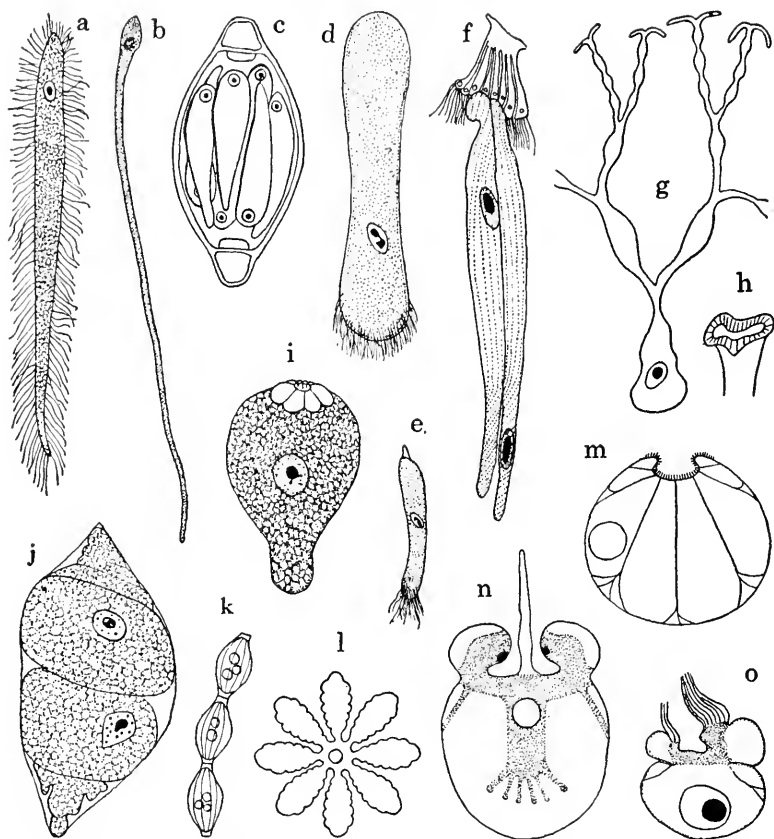


FIG. 176. a, *Rhynchocystis pilosa*, $\times 200$ (Hesse); b, c, *R. porrecta*: b, $\times 170$ (Hesse), c, spore, $\times 1330$ (Troisi); d, e, *Zygocystis wenrichi* (d, $\times 45$; e, $\times 450$) (Troisi); f, *Pleurocystis cuenoti*, $\times 190$ (Hesse); g, h, *Aikinetocystis singularis* (h, $\times 320$) (Gates); i-k, *Stomatophora coronata* (i, j, $\times 430$; k, $\times 870$) (Hesse); l, *Astrocystella lobosa*, $\times 120$ (Cognetti); m, *Craterocystis papua*, $\times 65$ (Cognetti); n, *Choanocystella tentaculata*, $\times 570$ (Cognetti); o, *Choanocystoides costaricensis*, $\times 470$ (Cognetti).

Pheretima wendessiana (New Guinea); trophozoites about $360\text{--}390\mu$ in diameter.

Genus **Choanocystella** (*Choanocystis* Cognetti). Trophozoites solitary; rounded or ovate; anterior end with a mobile sucker and a tentacle bearing cytoplasmic hairs; myonemes. One species.

C. tentaculata C. (Fig. 176, n). In seminal vesicles of *Pheretima beaufortii* (New Guinea); trophozoites 50μ by 36μ .

Genus **Choanocystoides** Cognetti. Trophozoites solitary, rounded or cup-shaped; anterior end with a mobile sucker, bordered by cytoplasmic filaments. One species.

C. costaricensis C. (Fig. 176, o). In seminal vesicles of *Pheretima heterochaeta* (Costa Rica); trophozoites 40–45 μ in diameter; nucleus ovoid, large, 12 μ in diameter.

Genus **Beccaricystis** Cognetti. Mature trophozoites elongate, cylindrical, with a sucker-like depression at anterior end; nucleus at its bottom. One species.

B. lorai C. (Fig. 177, a). In seminal vesicles of *Pheretima sermowaiana*; trophozoites cylindrical, with wart-like growths, myonemes run lengthwise with radially arranged transverse fibrils; about 100 μ long.

Genus **Albertisella** Cognetti. Mature trophozoites cup-shaped, with anterior sucker with a smooth wall; nucleus at its bottom. One species.

A. crater C. In seminal vesicles of *Pheretima sermowaiana*.

Family 6 Schaudinnellidae Poche

Parasitic in the digestive system of oligochaetes; spores spherical; trophozoites do not encyst; male trophozoites producing microgametes and female, macrogametes; zygotes or amphionts (spores) rounded.

Genus **Schaudinnella** Nusbaum. Trophozoites elongate spindle, free in lumen or attached to gut wall; sporadins male or female; spherical macrogametes and fusiform microgametes; zygotes or amphionts encapsulated, passed out of host or enter gut epithelium, dividing to produce many sporozoites (autoinfection).

S. henleae N. (Fig. 177, b, c). In gut of *Henlea leptodera*; mature trophozoites about 70 μ by 9 μ ; attached trophozoite with a clear wart-like epimerite; female and male sporadins; macrogametes, 5–7.5 μ in diameter; microgametes, spindle-form, 1–1.25 μ long; sporozoites rounded oval, 2.5–3 μ in diameter.

Family 7 Diplocystidae Bhatia

Coelomic or gut parasites of insects; trophozoites solitary or associated early in pairs; spores round or oval, with 8 sporozoites.

Genus **Diplocystis** Kunstler. Trophozoites spherical to oval; association of 2 individuals begin early in spherical form; spores round or oval, with 8 sporozoites; in coelom of insects.

D. schneideri K. (Fig. 177, d, e). In general body cavity of *Periplaneta americana*; young stages in gut epithelium; cysts up to 2 mm. in diameter; spores 7–8 μ in diameter; sporozoites 16 μ long.

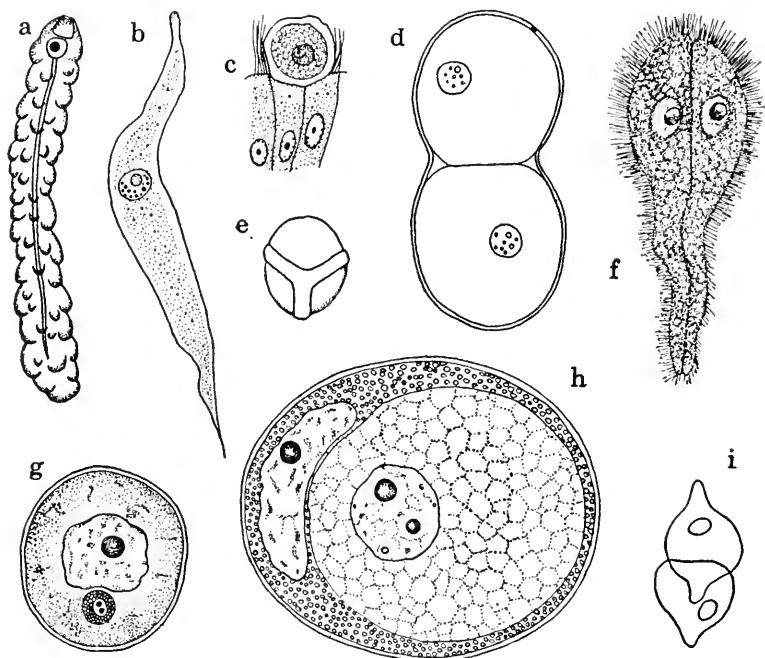


FIG. 177. a, *Beccaricystis loriai*, $\times 570$ (Cognetti); b, c, *Schaudinnella henleae* (b, $\times 885$; c, $\times 1000$) (Nusbaum); d, e, *Diplocystis schneideri* (d, $\times 14$; e, $\times 2000$) (Kunstler); f, *Urospora chiridotae*, $\times 200$ (Pixell-Goodrich); g-i, *Gonospora minchini* (g, a young trophozoite in host egg; h, a mature trophozoite, $\times 330$; i, sporadins in association, $\times 80$) (Goodrich and Pixell-Goodrich).

Genus **Lankesteria** Mingazzini. Trophozoites more or less spatulate; spherical cyst formed by 2 laterally associated sporadins in rotation; spores oval, with flattened ends, with 8 sporozoites; in gut of tunicates, flatworms and insects. Several species.

L. culicis (Ross) (Fig. 174). In gut and Malpighian tubules of *Aedes aegypti* and *A. albopictus*; mature trophozoites about 150–200 μ by 31–41 μ ; cysts spherical, in Malpighian tubules of host, about 30 μ in diameter; spores 10 μ by 6 μ .

Family 8 **Urosporidae** Woodcock

Coelomic parasites in various invertebrates; sporadins associative; spores with unequal ends; with or without episporos of various forms, with 8 sporozoites.

Genus **Urospora** Schneider. Large; frequently in lengthwise association of 2 individuals of unequal sizes; spores oval, with a long filamentous process at one end; in body cavity or blood vessel of Tubifex, Nemertinea, Sipunculus, Synapta, and Chiridota. Several species.

U. chiridotae (Dogiel) (Fig. 177, *f*). In blood vessel of *Chiridota laevis* (in Canada); paired trophozoites up to about 1 mm. long; with stiff hairs.

Genus **Gonospora** Schneider. Trophozoites polymorphic, oval, pyriform or vermiform; cysts spherical; spore with a funnel at one end, rounded at the other; in gut, coelom or ova of polychaetes.

G. minchini Goodrich et Pixell-Goodrich (Figs. 177, *g-i*; 178, *g*). In coelom of *Arenicola ecaudata*; young trophozoites live in host eggs which float in the coelomic fluid; fully grown trophozoites leave eggs in which they grow up to 200 μ long, and encyst together in pairs; spores without well-developed funnel, 8–10 μ long.

Genus **Lithocystis** Giard. Trophozoites large, ovoid or cylindrical; attached for a long period to host tissue; pellicle with hair-like processes; endoplasm with calcium oxalate crystals; spores ovoid, with a long process at one end; in coelom of echinids.

L. brachycercus Pixell-Goodrich (Fig. 178, *a, b*). In coelom of *Chiridota laevis* (Canada); fully grown spherical trophozoites up to 200 μ in diameter; spore with a short projection at one end.

Genus **Pterospora** Racovitza et Labbé. Sporadins associative or solitary; free end drawn out into 4 bifurcated processes; cysts spherical or oval; spores with episporos drawn out into 3 lateral processes; in coelom of polychaetes.

P. maldaneorum R. et L. (Fig. 178, *c, d*). In coelom of *Liocephalus liopygus*; trophozoites about 140 μ long; cysts 288 μ by 214 μ ; episporos 24 μ in diameter; endospore 10–14 μ by 3–4 μ .

Genus **Ceratospora** Léger. Sporadins elongate conical, head to head association; without encystment; spores oval with a small collar at one end and 2 divergent elongate filaments at other. One species.

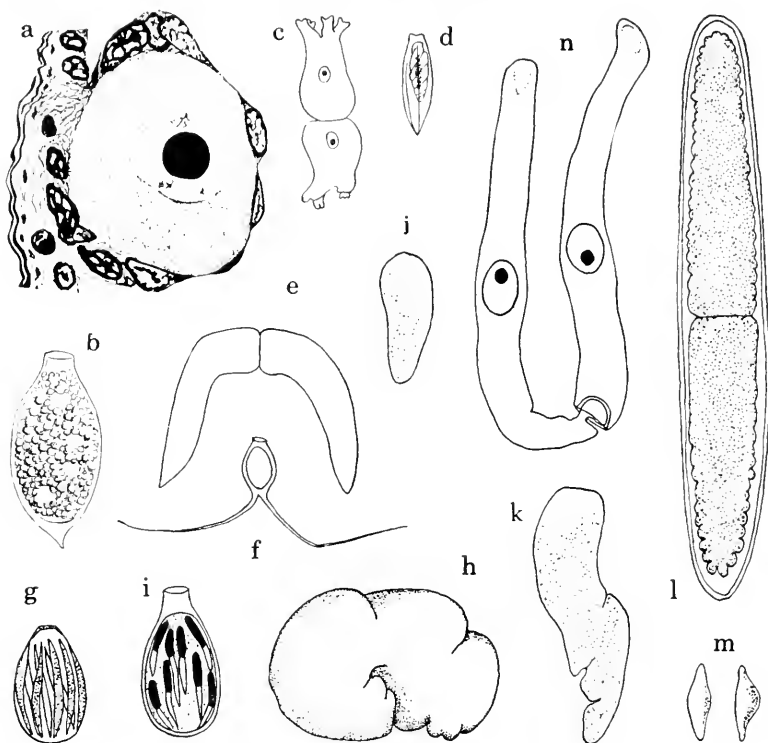


FIG. 178. a, b, *Lithocystis brachycereus*, $\times 1330$ (Pixell-Goodrich); c, d, *Pterospira maldaneorum* (c, $\times 40$; d, $\times 530$) (Labbé); e, f, *Ceratospira mirabilis* (e, $\times 45$; f, $\times 670$) (Léger); g, *Gonospora minchini*, $\times 2000$ (Goodrich); h, i, *Cystobia irregularis* (h, $\times 65$; i, $\times 770$) (Minchin); j-m, *Allantocystis dasyhelei* (j-l, $\times 500$; m, $\times 560$) (Keilin); n, *Ganymedes anaspides*, $\times 570$ (Huxley).

C. mirabilis L. (Fig. 178, e, f). Sporadins $500-600\mu$ long; spore 12μ by 8μ , filaments 34μ long; in general body cavity of *Glycera* sp.

Genus **Cystobia** Mingazzini. Trophozoites, large, irregular; fully grown forms always with 2 nuclei, due to early union of 2 individuals; spores oval, membrane drawn out and truncate at one end; in blood vessels and coelom of *Holothuria*.

C. irregularis (Minchin) (Fig. 178, h, i). Trophozoites irregular in form; up to 500μ long; endoplasm opaque, granulated; cysts in connective tissue of vessels; spore ovoid, epispore bottle-like, 25μ long; in blood vessel of *Holothuria nigra*.

Family 9 **Allantocystidae** Bhatia

Trophozoites elongate cylindrical; cysts elongate, sausage-like; spores fusiform, sides slightly dissimilar.

Genus **Allantocystis** Keilin. Sporadins, head to head association; cysts sausage-like; in dipterous insects. One species.

A. dasyhelei K. (Fig. 178, *j-m*). In gut of larval *Dasyhelea obscura*; full-grown sporadins 65–75 μ by 20–22 μ ; cysts 140–150 μ by 20 μ ; spores 18 μ by 6.5 μ .

Family 10 **Ganymedidae** Huxley

Trophozoites only known; mature individuals biassociative; posterior end of primate with a cup-like depression to which the epimeritic organella of satellite fits; cysts spherical; spores unknown.

Genus **Ganymedes** Huxley. Characters of the family; Huxley considers it as an intermediate form between *Acephalina* and *Cephalina*.

G. anaspides H. (Fig. 178, *n*). In gut and liver-tube of the crustacean, *Anaspides tasmaniae* (Tasmania); trophozoites in association, 70–300 μ by 60–130 μ ; cysts 85–115 μ in diameter.

Tribe 2 **Cephalina** Delage

The body of a trophozoite is divided into the protomerite and deutomerite by an ectoplasmic septum; inhabitants of the alimentary canal of invertebrates, especially arthropods.

One host species involved

Non-septate; epimerite a knob. Family 1 *Lecudinidae* (p. 392)
Septate

Development intracellular

Sporadins associative. Family 2 *Cephaloidophoridae* (p. 393)

Sporadins solitary. Family 3 *Stenophoridae* (p. 393)

Development extracellular

Sporadins associative

Satellite non-septate. Family 4 *Didymophyidae* (p. 393)

Satellite septate. Family 5 *Gregarinidae* (p. 394)

Sporadins solitary

Epimerite simple knob-like

Cysts with several ducts. Family 6 *Leidymanidae* (p. 396)

Cysts without or with one duct.

. Family 7 *Monoductidae* (p. 396)

Epimerite not simple knob-like

Epimerite cup-shaped or digitate

Epimerite cup-shaped. Family 8 *Menosporidae* (p. 398)

- Epimerite digitate... Family 9 Dactylophoridae (p. 398)
 Epimerite otherwise
 Spore hat-shaped... Family 10 Stylocephalidae (p. 401)
 Spore of other shapes
 Spore with spines.....
 Family 11 Acanthosporidae (p. 401)
 Spore without spines.....
 Family 12 Actinocephalidae (p. 403)
 Two host species involved..... Family 13 Porosporidae (p. 407)

Family 1 **Lecudinidae** Kamm

Epimerite simple, symmetrical; non-septate; spores ovoidal, thickened at one pole; solitary; in gut of polychaetes and termites. Undoubtedly intermediate forms between Acephalina and Cephalina.

Genus **Lecudina** Mingazzini. Epimerite simple, knob-like; in polychaetes.

L. pellucida (Kölliker) (Fig. 179, *a*). In *Nereis cultrifera* and *N. beaucourdrayi*; trophozoites ellipsoid; spores 7μ by 5μ .

Genus **Polyrhabdina** Mingazzini. Trophozoites flattened, ovoidal; epimerite with a corona of processes with split ends, deeply stainable; in polychaetes, Spionidae.

P. spionis (Kölliker) (Fig. 179, *b*). In *Scololepis fuligionosa*; 100μ by 35μ ; epimerite with a corona of 8–10 processes; cysts(?).

Genus **Kofoidina** Henry. Epimerite rudimentary; development intracellular; 2–14 sporadins in association; cysts and spores unknown.

K. ovata H. In midgut of *Zootermopsis angusticollis* and *Z. nevadensis*; syzygy 153 – 672μ long; sporadins 41 – 105μ long.

Genus **Sycia** Léger. Epimerite knobbed, bordered by a thick ring; protomerite subspherical; deutomerite conical, with navicular inclusions; in marine annelids.

S. inspinata L. (Fig. 179, *c*). In *Audouinia lamarcki*.

Genus **Zygosoma** Labbé. Trophozoites with wart-like projections; epimerite a simple knob; spores oval; in gut of marine annelids.

Z. globosum Noble (Fig. 179, *d, e*). Trophozoites 250 – 500μ by 200 – 380μ ; epimerite a large globule; cysts 400μ by 360μ , without ducts; spores oval, with 4 sporozoites, 9μ by 7μ ; reduction post-zygotic, 6 chromosomes; in gut of *Urechis caupo* in California.

Genus **Ulivina** Mingazzini. Elongate ellipsoid; epimerite simple, spores unknown; in gut of polychaetes.

U. rhynchoboli (Crawley). Sporadins up to 700μ long; in *Rhynchobolus americanus*.

Family 2 Cephaloidophoridae Kamm

Development intracellular; early association; cysts without sporoducts; spores ovoidal, with equatorial line; in gut of Crustacea.

Genus **Cephaloidophora** Mawrodiadi. Sporadins biassociative, early; epimerite rudimentary; cysts without sporoducts; spores in chain, ovoidal.

C. olivia (Watson) (Fig. 179, *f*). Biassociated sporadins up to 218μ long; individuals up to 118μ by 36μ ; cysts spheroidal, 60μ in diameter; spores(?); in gut of *Libinia dubia*; Long Island.

C. nigrofusca (Watson). Sporadins, ovoid to rectangular, up to 125μ by 75μ ; cysts and spores(?); in gut of *Uca pugnax* and *U. pugilator*.

Family 3 Stenophoridae Léger et Duboseq

Development intracellular; sporadins solitary; with a simple epimerite or none; cysts open by rupture; spores ovoid, with or without equatorial line, not extruded in chain; in Diplopoda.

Genus **Stenophora** Labbé. With or without simple epimerite; spores ovoid with equatorial line, not in chain.

S. larvata (Leidy) (Fig. 179, *g*). Sporadins up to 800μ by 23μ ; protomerite small; in gut of *Spirobolus spinigerus* at Philadelphia.

S. robusta Ellis (Fig. 179, *h*). Sporadins 140 – 180μ by 67μ ; cysts and spores both unobserved; in gut of *Parajulus venustus*, *Orthomorpha gracilis* and *O. sp.*; Colorado.

Genus **Fonsecaia** Pinto. Spores elongate ovoid; without equatorial line; without endospore.

F. polymorpha Pinto (Fig. 179, *i, j*). Sporadins 170μ long; spores 18μ by 8μ ; in gut of *Orthomorpha gracilis*; Brazil.

Family 4 Didymophyidae Léger

2–3 sporadins in association; satellite without septum.

Genus **Didymophyes** Stein. Epimerite a small pointed papilla; cysts spherical, open by rupture; spores ellipsoidal.

D. gigantea S. Sporadins slender, 1 cm. by 80 – 100μ ; 2 deutomerites; cysts spherical, 600 – 700μ in diameter; spores oval, 6.5μ by 6μ ; in gut of larvae of *Oryctes nasicornis*, *O. sp.*, and *Phyllognathus sp.*

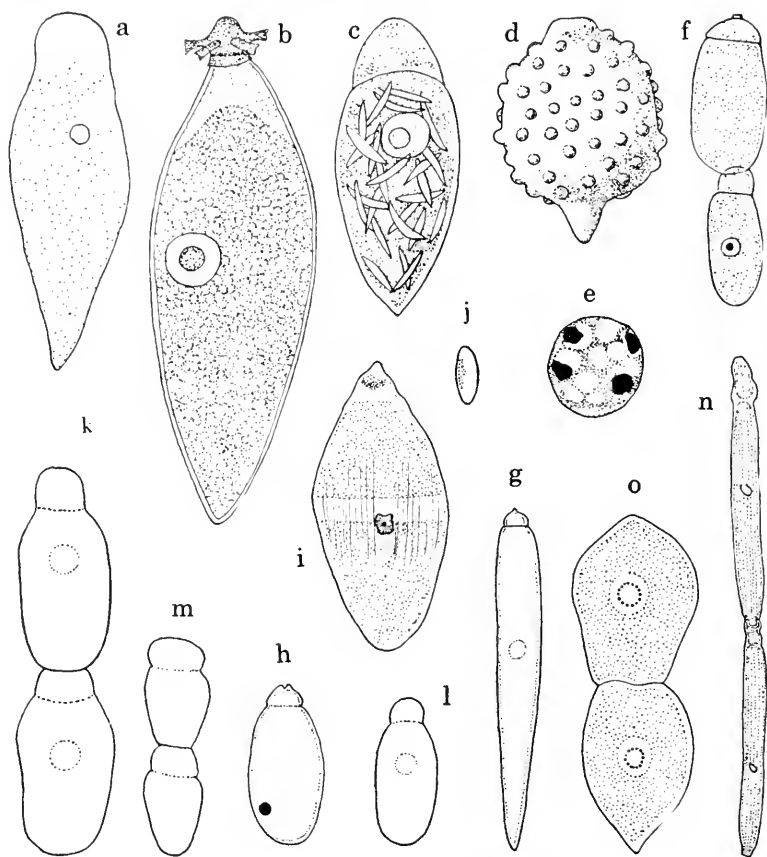


FIG. 179. a, *Lecudina pellucida* (Kölliker); b, *Polyrhabdina spionis*, $\times 800$ (Reichenow); c, *Sycia inspinata* (Léger); d, e, *Zygosoma globosum* (d, $\times 60$; e, $\times 1260$) (Noble); f, *Cephaloidophora olivia*, $\times 190$ (Kamm); g, *Stenophora larvata*, $\times 50$ (Leidy); h, *S. robusta*, $\times 130$ (Ellis); i, j, *Fousecaia polymorpha* (i, $\times 220$; j, $\times 430$) (Pinto); k, *Gregarina blattarum*, $\times 55$ (Kudo); l, *G. locustae*, $\times 65$ (Leidy); m, *G. oriceps*, $\times 30$ (Crawley); n, *Protomagalhaesia serpentula*, $\times 35$ (Pinto); o, *Gamocystis tenax* (Schneider).

Family 5 Gregarinidae Labbé

Sporadins in association; epimerite simple, symmetrical; cysts with or without ducts; spores symmetrical.

Genus **Gregarina** Dufour. Sporadins biassociative; epimerite small, globular or cylindrical; spores dolioform to cylindrical;

cysts open by sporoducts; in gut of arthropods. Numerous species.

G. blattarum Siebold (Fig. 179, *k*). Sporadins in syzygy, 500–1100 μ by 160–400 μ ; cysts spherical or ovoidal; 8–10 sporoducts; spores cylindrical to dolioform, truncate at ends, 8–8.5 μ by 3.5–4 μ ; in gut of the cockroach.

G. locustae Lankester (Fig. 179, *l*). Sporadins 150–350 μ long; syzygy; in *Dissosteria carolina*.

G. oviceps Diesing (Fig. 179, *m*). Sporadins up to 500 μ by 225 μ ; in syzygy; spherical cysts 250 μ in diameter; 2–5 sporoducts up to 1 mm. long; spores dolioform, 4.5 μ by 2.25 μ ; in *Gryllus abbreviatus* and *G. americanus*.

Genus **Protomagalhaesia** Pinto. Sporadins cylindrical; in syzygy, protomerite of satellite draws in the posterior end of primate; cysts without ducts; spores dolioform, with spines at ends.

P. serpentula (Magalhães) (Fig. 179, *n*). Sporadins up to 1.2 mm. by 180 μ ; in gut and coelom of *Blatta orientalis*.

Genus **Gamocystis** Schneider. Septate only in trophozoites; sporadins non-septate; in syzygy; spore formation partial; with sporoducts; spores cylindrical. A few species.

G. tenax S. (Fig. 179, *o*). Association head to head; spherical cysts with 15 or more ducts; spore cylindrical, with rounded ends; in gut of *Blattella lapponica*.

Genus **Hyalospora** Schneider. Sporadins in syzygy; cytoplasm yellowish orange; epimerite a simple knob; cysts open by rupture; spores fusiform.

H. affinis S. Trophozoites 300 μ long; cysts, yellow, 60 μ in diameter; spores 8.7 μ by 6 μ ; in gut of *Machilis cylindrica*.

Genus **Hirmocystis** Labbé. Sporadins associative, 2–12 or more; with a small cylindrical papilla-like epimerite; cysts without ducts; spores ovoidal.

H. harpali Watson (Fig. 180, *a*). Total length of association up to 1060 μ ; sporadins up to 560 by 80 μ ; cysts unknown; in gut of *Harpalus pennsylvanicus erythropus*.

H. termitis (Leidy) (Fig. 180, *b*). Association 614–803 μ long; epimerite in cephalins simple sphere; cysts rare; spores (?); in *Zootermopsis angusticollis*, *Z. nevadensis*, etc.

Genus **Uradiophora** Mercier. Sporadins in syzygy; deutomerite with small process; epimerite an elongate papilla; cysts oval without ducts; spores spherical, in chains.

U. cuenoti M. 2-4 sporadins in syzygy; individuals up to 700μ long; cysts ovoid, 44μ long; spores 4μ in diameter; in gut of *Atyaephyra desmarcesti*.

Genus **Pyxinoides** Trégouboff. Sporadins biassociative; epimerite with 16 longitudinal furrows, small cone at end.

P. balani (Kölliker). Primate up to 130μ ; satellite 60μ long; in gut of *Balanus amphitrite* and *B. eburneus*.

Genus **Anisolobus** Vincent. Sporadins in syzygy; epimerite lacking in cephalins; protomerite of primate expanded to form sucker-like organella; cysts ellipsoid, with thick envelope; with 6-8 sporoducts; spores barrel-shaped. One species.

A. dacnecola V. (Fig. 180, c). In midgut of *Dacne rufifrons*; 2 sporadins in syzygy $100-300\mu$ by $20-50\mu$; cysts without envelope, $130-150\mu$ by $80-90\mu$; sporoducts $40-50\mu$ long; spores in chain, dolioform, 6μ by 4μ .

Genus **Carcinoectes** Ball. Sporadins in syzygy of 2 or more individuals; epimerite rudimentary; cysts without sporoducts; spores round to ovoidal, not in chain; in gut of Crustacea.

C. hesperus B. (Fig. 180, d, e). 2-6 sporadins in association; sporadins up to 320μ by 9μ ; cysts about 140μ by 123μ , attached to the wall of hindgut; spores 8.6μ by 7.7μ , with 8 radially arranged sporozoites; in gut of *Pachygrapsus crassipes* in California.

Family 6 **Leidyaniidae**

Similar to the last two families; but sporadins are solitary and epimerite simple knob-like; cysts with several sporoducts.

Genus **Leidyana** Watson. Solitary; epimerite a simple globular sessile knob; cysts with ducts; spores dolioform.

L. erratica (Crawley) (Fig. 180, f). Sporadins up to 500μ by 160μ ; cysts about 350μ in diameter; membrane about 30μ thick; 1-12 sporoducts; spores extruded in chains, 6μ by 3μ ; in gut of *Gryllus abbreviatus* and *G. pennsylvanicus*.

Family 7 **Monoductidae** Ray et Chakravatry

As in the last family solitary; but cyst with a single sporoduct or none; spore with 8 sporozoites.

Genus **Monoductus** R. et C. Sporadins solitary; epimerite a small elevation with prongs attached to its base; anisogamy; cyst with a single sporoduct; spores flattened fusiform, with dissimilar ends, each with 8 sporozoites. One species.

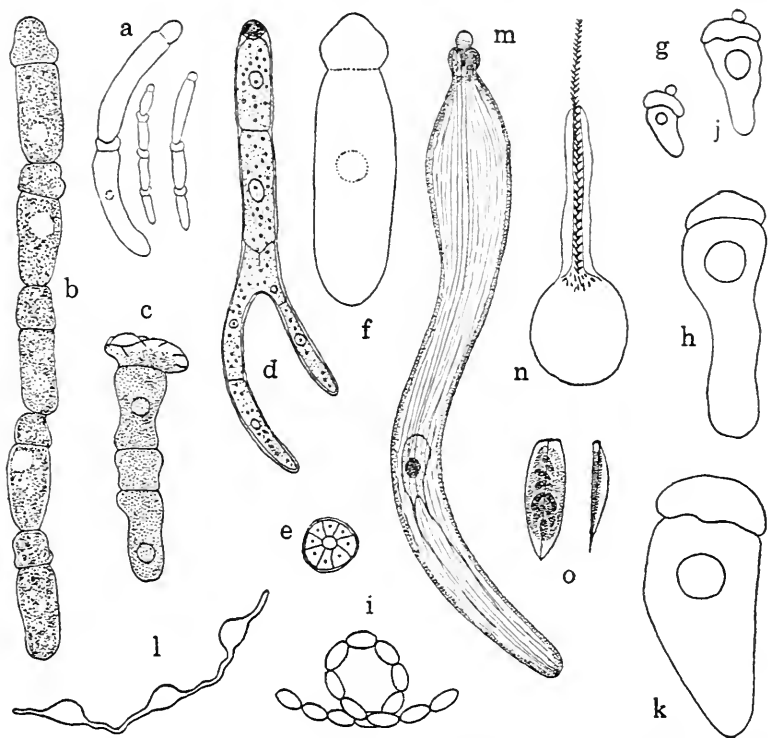


FIG. 180. a, *Hirmocystis harpali*, $\times 50$ (Watson); b, *H. termitis*, $\times 85$ (Henry); c, *Anisolobus dacnecola*, $\times 270$ (Vincent); d, e, *Carcinocetes hesperus* (d, $\times 200$; e, $\times 780$) (Ball); f, *Leydiana erratica*, $\times 170$ (Watson); g-i, *Lepismatophila thermobiae* (g, h, $\times 85$; i, spores, $\times 200$) (Adams and Travis); j-l, *Colepismatophila watsonae* (j, k, $\times 85$; l, spores, $\times 200$) (Adams and Travis); m-o, *Monoductus lunatus* (m, cephalin, $\times 240$; n, cyst, $\times 120$; o, two views of spore, $\times 2330$) (Ray and Chakravatry).

M. lunatus R. et C. (Fig. 180, m-o). Cephalins $225-445\mu$ by $33-47\mu$; epimerite with about 16 prongs; nucleus parachute-shaped, with myonemes attached at posterior margin; sporadins develop posterior pseudopodial processes before association; cysts spherical, $225-230\mu$ in diameter, voided by host; development completed in 3-4 days outside the host body, with one duct; spores 10.25μ by 4μ , truncate at one end, attenuated at other and discharged in a single chain; in gut of *Diplopoda* sp.

Genus **Sphaerocystis** Léger. Sporadins solitary; without protoemerite; spherical.

S. simplex L. Sporadins $100\text{--}140\mu$ in diameter; protomerite in young trophozoites; spherical cysts in which individuals are not associative, 100μ in diameter; spores ovoid, 10.5μ by 7.5μ ; in gut of *Cyphon pallidulus*.

Genus **Lepismatophila** Adams et Travis. Epimerite a simple knob; cysts without ducts; spores ellipsoidal, smooth, in chain. One species.

L. thermobiae A. et T. (Fig. 180, *g-i*). Sporadins $67\text{--}390\mu$ by $30\text{--}174\mu$; cysts white to black, ellipsoidal to subspherical, $244\text{--}378\mu$ by $171\text{--}262\mu$; spores brown, 13.6μ by 6.8μ ; in ventriculus of *Thermobia domestica*.

Genus **Colepismatophila** Adams et Travis. Similar to the last genus; but larger; spores in wavy chains, hat-shaped, with 2 curved filamentous processes attached at opposite ends. One species.

C. watsonae A. et T. (Fig. 180, *j-l*). Sporadins $92\text{--}562\mu$ by $55\text{--}189\mu$; cysts $226\text{--}464\mu$ by $158\text{--}336\mu$; spores 16.5μ by 9.7μ , processes 21μ long; in ventriculus of *Thermobia domestica*.

Family 8 Menosporidae Léger

Sporadins solitary; epimerite a large cup, bordered with hooks, with a long neck; cysts without sporoducts; spores crescentic, smooth.

Genus **Menospora** Léger. With the characters of the family.

M. polyacantha L. (Fig. 181, *a, b*). Sporadins $600\text{--}700\mu$ long; cysts 200μ in diameter; spores 15μ by 4μ ; in gut of *Agrion puella*.

Family 9 Dactylophoridae Léger

Sporadins solitary; epimerite complex, digitate; cysts dehiscence by pseudocyst; spores cylindrical; in gut of chilopods.

Genus **Dactylophorus** Balbiani. Protomerite wide, bordered by digitiform processes; spores cylindrical.

D. robustus Léger (Fig. 181, *c, d*). Sporadins $700\text{--}800\mu$ long; cysts spherical, 200μ in diameter; spores 11μ by 4.3μ ; in gut of *Cryptops hortensis*.

Genus **Echinomera** Labbé. Epimerite an eccentric cone with 8 or more digitiform processes; cysts without sporoducts; spores cylindrical.

E. magalhaesi (Pinto) (Fig. 181, *e*). Sporadins up to 300μ by 70μ ; in gut of *Scolopendra* sp.

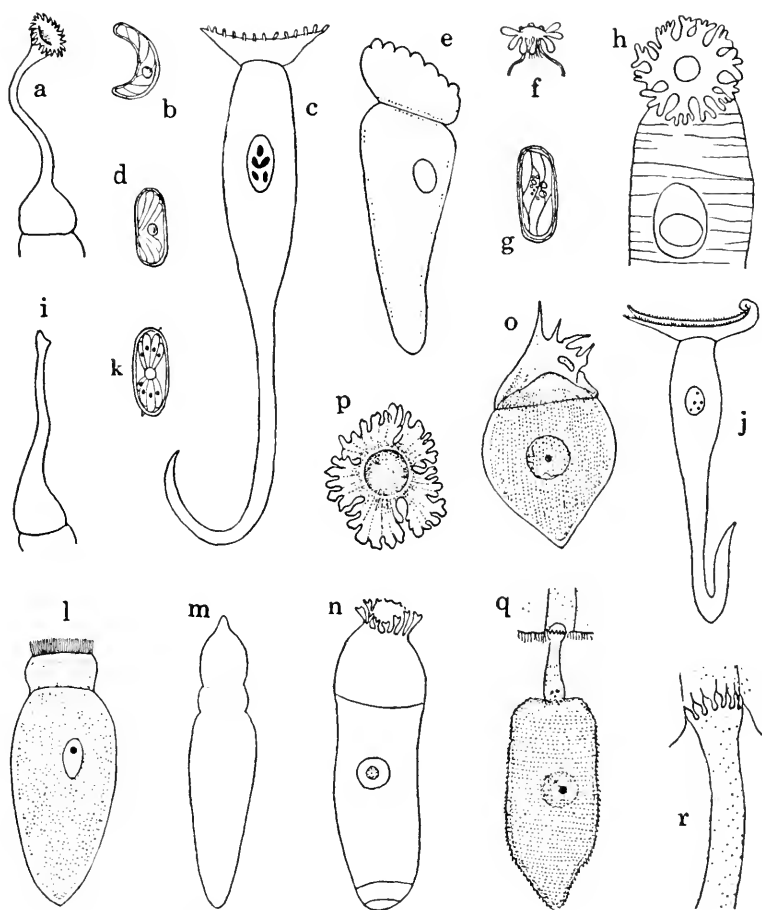


FIG. 181. a, b, *Menospora polyacantha* (Léger); c, d, *Dactylophorus robustus* (c, $\times 130$; d, $\times 900$) (Léger); e, *Echinomera magalhaesi*, $\times 130$ (Pinto); f, g, *Rhopalonia hispida* (g, $\times 830$) (Léger); h, *Dendrorhynchus systemi*, $\times 770$ (Keilin); i, *Trichorhynchus pulcher* (Schneider); j, k, *Nina gracilis* (j, $\times 10$) (Schneider); l, *Seticephalus elegans*, $\times 450$ (Pinto); m, *Acutispora macrocephala*, $\times 65$ (Crawley); n, *Metamera schubergi*, $\times 270$ (Duke); o, p, *Hentschelia thalassemae* (o, $\times 230$; p, $\times 620$) (Mackinnon and Ray); q, r, *Lecythion thalassemae* (q, $\times 270$; r, $\times 930$) (Mackinnon and Ray).

Genus **Rhopalonia** Léger. Epimerite spherical, with 10 or more digitiform processes; pseudocysts; spores cylindrical.

R. hispida (Schneider) (Fig. 181, f, g). Endoplasm yellowish

orange; cysts 200–250 μ in diameter; spores 16 μ by 6.5 μ ; in gut of *Geophiles* sp. and *Stigmatogaster gracilis*.

Genus **Dendrorhynchus** Keilin. Elongate; epimerite a disc, surrounded by numerous ramified papillae; transverse fibrils conspicuous; cysts elliptical; spores fusiform.

D. systemi K. (Fig. 181, h). Sporadins 255 μ by 18.5–20 μ ; spores 18–19 μ by 7 μ ; in midgut of larvae of *Systemus* sp., a dolichopodid fly, found in decomposed sap of elm tree.

Genus **Trichorhynchus** Schneider. Protomerite prolonged anteriorly into a long neck, dilated at tip; pseudocyst; spores cylindrical to ellipsoidal.

T. pulcher S. (Fig. 181, i). Cysts 303–316 μ in diameter; spores 9.7 μ by 5.8 μ ; in gut of *Scutigera* sp.

Genus **Nina** Grebnecki (*Pterocephalus* Schneider). Protomerite made up of 2 long narrow horizontal lobes fused and upturned spirally at one end, peripheral portion with many teeth, from which project long filaments; spores in chain; in gut of myriapods.

N. gracilis G. (Fig. 181, j, k). 4–5 mm. long; cysts spherical; spores ellipsoidal, in chain; in gut of *Scolopendra cingulata*.

Genus **Seticephalus** Kamm. Protomerite with closely set brush-like bristles.

S. elegans (Pinto) (Fig. 181, l). Sporadins up to 75 μ by 35 μ ; cysts and spores unknown; in gut of *Scolopendra* sp.

Genus **Acutispora** Crawley. Solitary; pseudocyst; spore biconical, with a thick blunt endosporal rod at each end. One species.

A. macrocephala C. (Fig. 181, m). Sporadins up to 600 μ long; cysts spherical, 410 μ in diameter; spores navicular, slightly curved, 19 μ by 4 μ ; in gut of *Lithobius forficatus*.

Genus **Metamera** Duke. Epimerite eccentric, bordered with many branched digitiform processes; cysts without ducts; spores biconical.

M. schubergi D. (Fig. 181, n). Sporadins 150 μ by 45 μ ; spores 9 μ by 7 μ ; in gut of *Glossosiphonia complanata* and *Placobdella marginata*.

Genus **Hentschelia** Mackinnon et Ray. Epimerite with a short neck, umbrella-like with its margin divided into 4–5 lobes, each fluted on anterior surface; 2 sporadins encyst together; gametes anisogamous; flagellate and non-flagellate; zygote gives rise to a spherical spore with 8 sporozoites. One species.

H. thalassemae M. et R. (Fig. 181, *o*, *p*). Cephalins $75\text{--}98\mu$ by $30\text{--}45\mu$; in gut of *Thalassema neptuni*.

Genus **Lecythion** Mackinnon et Ray. Epimerite a low cone, surrounded by 14–15 petal-shaped lobes, with a neck; cysts and spores unknown.

L. thalassemae M. et R. (Fig. 181, *q*, *r*). Cephalins 135μ by 52μ ; epimerite about 27μ long; in gut of *Thalassema neptuni*.

Family 10 **Stylocephalidae** Ellis

Sporadins solitary; epimerite varied; pseudocysts; hat-shaped spores in chains.

Genus **Stylocephalus** Ellis. Epimerite nipple-like; cysts covered with papillae; in arthropods and molluscs.

S. giganteus E. (Fig. 182, *a*). Sporadins 1.2–1.8 mm. long; cysts spherical, 450μ in diameter; spores subspherical black, 11μ by 7μ ; in *Eleodes* sp., *Asida opaca*, *A.* sp., and *Eusattus* sp. (Coleoptera).

Genus **Bulbocephalus** Watson. Epimerite a dilated papilla located in middle of a long neck.

B. elongatus W. (Fig. 182, *b*). Sporadins up to 1.6 mm. by 50μ ; nucleus diagonal; cysts and spores unknown; in gut of *Cucujus* larva (a coleopteran).

Genus **Sphaerorhynchus** Labbé. Epimerite a small sphere at end of a long neck.

S. ophioides (Schneider). Cephalins 1.3 mm.; epimerite 220μ long; terminal part 8.5μ ; sporadins 3–4 mm. long; in gut of *Acis* sp.

Genus **Cystocephalus** Schneider. Epimerite a large lance-shaped papilla with a short neck; spore hat-shaped.

C. algerianus S. (Fig. 182, *c*, *d*). Sporadins 3–4 mm. long; spores $10\text{--}10.5\mu$ long; in gut of *Pimelia* sp.

Genus **Lophocephalus** Labbé. Epimerite sessile crateriform disc with crenulate periphery, surrounded by digitiform processes.

L. insignis (Schneider) (Fig. 182, *e*). Sporadins 1 mm. long; cysts rounded; 430μ by 330μ ; pseudocysts; spores 10μ long; in gut of *Helops striatus*.

Family 11 **Acanthosporidae** Léger

Sporadins solitary; epimerite complex; cysts without sporoducts; spores with equatorial and polar spines.

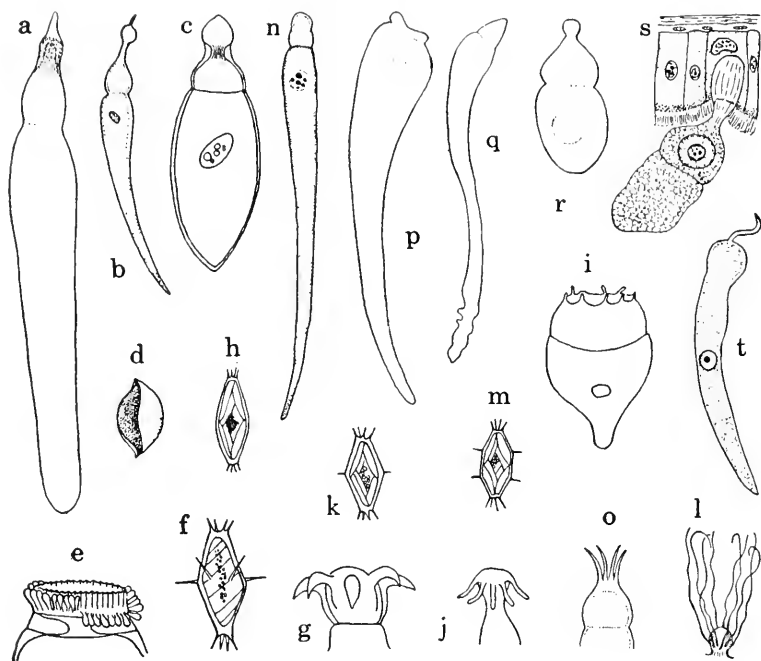


FIG. 182. a, *Stylocephalus giganteus*, $\times 65$ (Ellis); b, *Bulbocephalus elongatus*, $\times 15$ (Watson); c, d, *Cystocephalus algerianus* (c, $\times 6$; d, $\times 930$) (Schneider); e, *Lophocephalus insignis* (Schneider); f, *Acanthospora polymorpha*, $\times 1670$ (Léger); g, h, *Corycella armata* (h, $\times 860$) (Léger); i, *Prismatospora evansi*, $\times 50$ (Ellis); j, k, *Ancyrophora gracilis* (k, $\times 1250$) (Léger); l, m, *Cometoides capitatus* (m, $\times 1330$) (Léger); n, o, *Actinocephalus acutispina* (Léger); p, *Amphoroides calverti*, $\times 130$ (Watson); q, *Asterophora philica*, $\times 65$ (Leidy); r, *Steinina rotunda*, $\times 130$ (Watson); s, *Pileocephalus striatus*, $\times 180$ (Léger and Duboseq); t, *Stylocystis praecox*, $\times 80$ (Léger).

Genus **Acanthospora** Léger. Epimerite simple conical knob; spores with spines.

A. polymorpha L. (Fig. 182, f). Sporadins polymorphic; up to 1 mm. long; protomerite cylindro-conical; deutomerite ovoidal; endoplasm yellowish brown; cyst 500–700 μ in diameter; spore with 6 spines at each pole and at equatorial plane, 8 μ by 4.4 μ ; in gut of *Hydrous ceraboides*.

Genus **Corycella** Léger. Epimerite globular, with 8 hooks; spores biconical, with one row of polar spines.

C. armata L. (Fig. 182, g, h). Sporadins 280–300 μ long; cysts

spherical, 250μ in diameter; spores 13μ by 6.5μ ; in gut of larva of *Gyrinus natator*.

Genus **Prismatospora** Ellis. Epimerite subglobular with 8 lateral hooks; spores hexagonal, with one row of spines at each pole.

P. evansi E. (Fig. 182, *i*). Sporadins broadly conical, 400μ long; cysts 370μ in diameter; without sporoducts; spores with 6 long spines at each pole, 11μ by 5.8μ ; in gut of *Tramea lacerta* and *Symptetrum rubicundulum*; Michigan.

Genus **Ancyrophora** Léger. Epimerite globular with 5–10 digitiform processes directed posteriorly; spores biconical, with spines.

A. gracilis L. (Fig. 182, *j, k*). Sporadins 200μ –2 mm. long; cysts spherical, 200μ in diameter; spores hexagonal in optical section, with 4 polar and 6 equatorial spines, 8.5μ by 5μ ; in gut of larvae and adults of *Carabus auratus*, *C. violaceus*, *C. sp.*, and of larvae of *Silpha thoracica* (Coleoptera).

Genus **Cometoides** Labbé. Epimerite globular with 6–15 long filaments; spores with polar spines and 2 rows of equatorial spines.

C. capitatus (Léger) (Fig. 182, *l, m*). Sporadins up to 2 mm. long, active; epimerite with 12–15 filaments, 32 – 35μ long; cysts 300μ in diameter; spores 5.1μ by 2.5μ ; in gut of larvae of *Hydrous* sp. (Coleoptera).

Family 12 Actinocephalidae Léger

Sporadins solitary; epimerite variously formed; cysts without sporoducts; spores irregular, biconical or cylindro-biconical; in gut of insects.

Genus **Actinocephalus** Stein. Epimerite sessile or with a short neck, with 8–10 simple digitiform processes at its apex; spores biconical.

A. acutispora Léger (Fig. 182, *n, o*). Sporadins 1–1.5 mm. long; cysts ovoid. 550 – 600μ by 280μ ; spores, acutely pointed, of 2 sizes, 4.5μ by 2.8μ and 6.4μ by 3.6μ ; in gut of the coleopteran, *Silpha laevigata*.

Genus **Amphoroides** Labbé. Epimerite a globular sessile papilla; protomerite cup-shaped; spores curved; in myriapods.

A. calverti (Crawley) (Fig. 182, *p*). Sporadins up to 1670μ by 120μ ; cysts spherical, 380μ in diameter; spores unknown; in gut of *Callipus lactarius*.

Genus **Asterophora** Léger. Epimerite a thick horizontal disc

with a milled border and a stout style projecting from center; spore cylindrobiconical; in Neuroptera and Coleoptera.

A. philica (Leidy) (Fig. 182, *q*). Sporadins 300μ –2 mm. long; cysts and spores unknown; in gut of *Nyctobates pennsylvanica*.

Genus **Steinina** Léger et Duboseq. Solitary; epimerite a short motile digitiform process, changing into a flattened structure; spore biconical; in Coleoptera.

S. rotunda Watson (Fig. 182, *r*). Sporadins 180 – 250μ long; in gut of *Amara augustata* (Coleoptera).

Genus **Pileocephalus** Schneider. Epimerite lance-shaped, with a short neck.

P. striatus Léger et Duboseq (Fig. 182, *s*). Sporadins 150μ long; nucleus in protomerite; cysts spherical; in gut of larvae of *Ptychoptera contaminata*.

Genus **Stylocystis** Léger. Epimerite a sharply pointed, curved process; spores biconical.

S. praecox L. (Fig. 182, *t*). Sporadins up to 500μ long; cysts ovoidal, 200μ long; spores 8μ by 5μ ; in gut of larval *Tanypus* sp.

Genus **Discorhynchus** Labbé. Epimerite a large spheroidal papilla with collar and short neck; spores biconical, slightly curved.

D. truncatus (Léger) (Fig. 183, *a, b*). Sporadins 300μ long; cysts spherical, 140μ in diameter; in gut of larvae of *Sericostoma* sp.

Genus **Anthorhynchus** Labbé. Epimerite a large flattened fluted disc; spores biconical, chained laterally.

A. sophiae (Schneider) (Fig. 183, *c, d*). Cephalins up to 2 mm. long, with 200μ long epimerite; protomerite 150μ long; endoplasm opaque; spores 7μ by 5μ ; in gut of *Phalangium opilio*.

Genus **Sciadiophora** Labbé. Epimerite a large sessile disc with crenulate border; protomerite with numerous vertical laminations; spores biconical.

S. phalangii (Léger) (Fig. 183, *e–g*). Sporadins 2–2.5 mm. long; protomerite with 15–16 plates; cysts 500μ in diameter; spores 9μ by 5μ ; in gut of *Phalangium crassum* and *P. cornutum* (Arachnida).

Genus **Amphorocephalus** Ellis. Epimerite a sessile peripherally fluted disc set upon a short neck; protomerite constricted superficially; spores unknown.

A. amphorellus E. (Fig. 183, *h*). Sporadins 500 – 970μ long; in gut of *Scolopendra heros*.

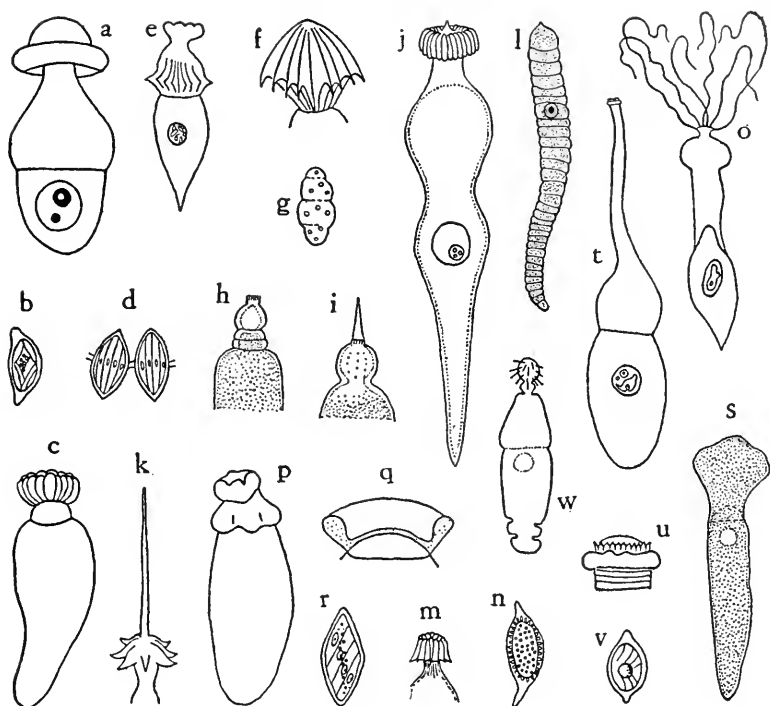


FIG. 183. a, b, *Discorhynchus truncatus* (a, $\times 130$) (Léger); c, d, *Anthorhynchus sophiae* (c, $\times 15$; d, $\times 1330$) (Schneider); e-g, *Sciadiophora phalangii* (g, spore, $\times 1040$) (Léger); h, *Amphorocephalus amphorellus* (Ellis); i, *Pyxinia bulbifera* (Watson); j, *Schneideria mucronata*, $\times 75$ (Léger); k, *Beloides firmus* (Léger); l, *Taeniocystis mira*, $\times 85$ (Léger); m, n, *Stictospora provincialis* (Léger); o, *Bothriopsis histrio* (Léger); p-r, *Coleorhynchus heros* (p, $\times 14$) (Schneider); s, *Legeria agilis* (Schneider); t-v, *Phialoides ornata* (t, $\times 45$; v, $\times 930$) (Léger); w, *Geneiorhynchus aescnae*, $\times 60$ (Crawley).

Genus **Pyxinia** Hammerschmidt. Epimerite flat crenulate crateriform disc; with a style in center; spores biconical.

P. bulbifera Watson (Fig. 183, i). Sporadins up to 850μ long; in gut of *Dermestes lardarius*.

Genus **Schneideria** Léger. Epimerite sessile, a thick horizontal disc with milled border; a style arising from center; sporadins without protomerite; spores biconical.

S. mucronata L. (Fig. 183, j). Sporadins $700-800\mu$ long; agile; polymorphic; cysts 270μ by 190μ ; spores fusiform, 15μ by 9μ ; in intestinal caeca of larvae of *Bibio marci*.

Genus **Beloides** Labbé. Epimerite bordered by pointed lateral processes and apical style; spores biconical.

B. firmus (Léger) (Fig. 183, *k*). Style 80μ long; cysts $180\text{--}200\mu$ in diameter; spores 14.5μ by 6μ ; in gut of larvae of *Dermestes lardarius*.

Genus **Taeniocystis** Léger. Epimerite sessile or with a short neck; 8–10 digitiform processes at its apex; deutomerite divided by septa into many chambers; spores biconical.

T. mira L. (Fig. 183, *l*). Sporadins tapeworm-like; $400\text{--}500\mu$ long; epimerite with 6–8 curved hooks; cysts spherical, 130μ in diameter; spores 7μ by 3μ ; in gut of larval *Ceratopogon solstitialis*.

Genus **Stictospora** Léger. Epimerite with a short neck, a spherical crateriform ball with 12 posteriorly-directed laminations set close to neck; cysts with a gelatinous envelope; without ducts; spores biconical, slightly curved.

S. provincialis L. (Fig. 183, *m, n*). Sporadins 1–2 mm. long; cysts 800μ in diameter; in gut of larvae of *Melolontha* sp. and *Rhizotrogus* sp.

Genus **Bothriopsis** Schneider. Epimerite sessile, small, oval, with 6 or more filamentous processes directed upward; spores biconical; cysts spherical.

B. histrio S. (Fig. 183, *o*). Epimerite with 6 filaments, $80\text{--}90\mu$ long; cysts $400\text{--}500\mu$ long; spores 7.2μ by 5μ ; in gut of *Hydaticus* sp.

Genus **Coleorhynchus** Labbé. Epimerite discoid, lower border over deutomerite; spores biconical.

C. heros (Schneider) (Fig. 183, *p-r*). Sporadins 2–3 mm. long; in gut of *Nepa cinerea*.

Genus **Legeria** Labbé. Protomerite wider than deutomerite; epimerite unknown; cysts without duct; spores cylindro-biconical.

L. agilis (Schneider) (Fig. 183, *s*). In gut of the larvae of *Colymbetes* sp.

Genus **Phialoides** Labbé. Epimerite a cushion set peripherally with stout teeth, surrounded by a wider collar; with a long neck; cysts spherical, without ducts; spores biconical.

P. ornata (Léger) (Fig. 183, *t-v*). Sporadins 500μ long; cysts $300\text{--}400\mu$ in diameter; spores 10.5μ by 6.7μ ; in gut of larvae of *Hydrophilus piceus*.

Genus **Geneiorhynchus** Schneider. Epimerite a tuft of short bristles at end of neck; spores cylindrical.

G. aeschnae Crawley (Fig. 183, *w*). Sporadins 420μ long; cysts and spores unknown; in *Aeschna constricta*.

Family 13 **Porosporidae** Léger

When naked or well-protected sporozoites enter the stomach and midgut of a specific crustacean host, they develop into typical cephaline gregarines; 1, 2, or more sporadins become associated and encyst. Repeated nuclear and cytoplasmic division results in formation of an enormous number of **gymnospores** in hindgut. Some observers consider this change as schizogony, and hence include the family in the suborder Schizogregarinaria. When the gymnospores are voided in the faeces of crustaceans and come in contact with molluscan host, they enter, or are taken in by phagocytosis of, the epithelial cells of the gills, mantle or digestive system. These gymnospores are especially found in abundance in the lacunae of the gills. Presently they become paired and fuse (Hatt); the zygotes develop into naked or encapsulated sporozoites within the phagocytes of the molluscan host, which when taken into a crustacean host, develop into cephaline gregarines.

Genus **Porospora** Schneider. Sporozoites formed in molluscan phagocytes without protective envelope (Hatt).

P. gigantea (van Beneden) (Fig. 184, *a-f*). Sporadins in *Homarus gammarus*, up to 10 mm. long; cysts 3–4 mm. in diameter; gymnospores spherical, 8μ in diameter (Hatt), containing some 1500 merozoites; in molluscan hosts, *Mytilus minimus* and *Trochocochelea mutabilis*, develop into naked sporozoites (17μ long) which are usually grouped within phagocytes.

Genus **Nematopsis** Schneider. Development similar to that of *Porospora* (Hatt); but each sporozoite in a double envelope.

N. legeri (de Beauchamp) (*Porospora galloprovincialis* Léger et Duboscq) (Fig. 184, *g-n*). Hatt (1931) carried on a very careful study of its development. Sporadins in a crustacean, *Eriphia spinifrons*, in linear or bifurcated syzygy, $75-750\mu$ long; cysts about 80μ in diameter; gymnospores 7μ in diameter, composed of fewer, but larger merozoites; permanent spores with a distinct one-piece shell (endospore) and a less conspicuous episporium, about $14-15\mu$ long and circular in cross-section, develop in numerous

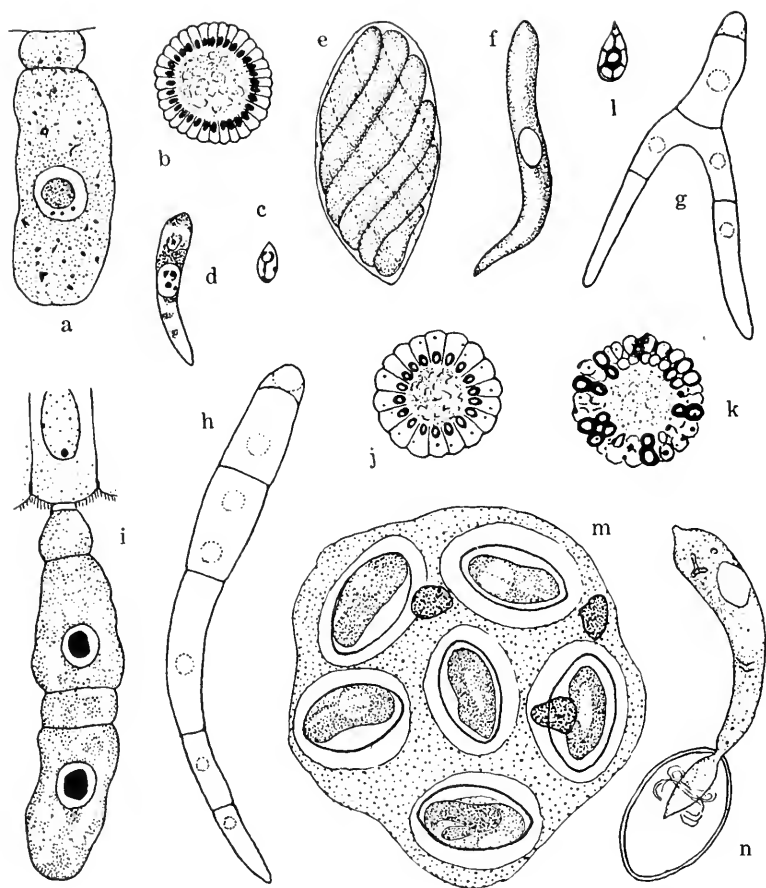


FIG. 184. a-f, *Porospora gigantea* (Hatt). a, a cephalin attached to *Homarus* gut, $\times 1250$; b, gymnospor; c, d, developing sporozoites in mollusc; e, sporozoites enveloped by phagocytes; f, a sporozoite, $\times 2250$. g-n, *Nematopsis legeri* (Hatt). g, h, trophozoites in *Eriphia*; i, associated trophozoites attached to gut-epithelium, $\times 1250$; j, gymnospor; k, gymnospor after entering molluscan body; l, a young sporozoite, $\times 2250$; m, cyst in mollusc with six spores; n, germination of a spore in *Eriphia* gut, $\times 1250$.

species of molluscan hosts: *Mytilus galloprovincialis*, *M. minimus*, *Lasea rubra*, *Cardita calyculata*, *Chiton caprearum*, *Trochocochlea turbinata*, *T. articulata*, *T. mutabilis*, *Phorcus richardi*, *Gibbula divaricata*, *G. rarilineata*, *G. adamsoni*, *Pisania maculosa*, *Ceri-*

thium rupestre, *Columbella rustica*, and *Conus mediterraneus* in European waters.

The author found in *Ostrea virginica* and other molluses in North Carolina, Virginia, and Maryland, this gregarine and was the first to demonstrate on this continent the germination of the spores taken from the infected oysters in the stomach and mid-gut of *Panopeus herbsti* and *Eurypanopeus depressus* at the Bureau of Fisheries Biological Laboratory at Beaufort, N. C. in July, 1936. The vermiform sporozoites emerge from the spores in the pyloric chamber of the stomach and more abundantly in the mid-gut of the mud crabs as early as thirty minutes after introduction of the infected tissues of the oyster into their mouths. In the brackish water of the middle Chesapeake Bay region of Maryland, the oyster and other molluscs are only slightly infected. The presence of the characteristic spores in oyster tissues is easily demonstrated by addition of 10 per cent sodium hydrate solution to the material on slides.

Suborder 2 **Schizogregarinaria** Léger

The schizogregarines are intestinal parasites of arthropods, annelids, and tunicates. When the spore gains entrance to the digestive tract of a specific host through mouth, it germinates and the sporozoites are set free (Fig. 185). These sporozoites develop into trophozoites either in the gut-lumen or within the host cells, and undergo schizogony (*c*), which may be binary or multiple fission or budding. The fully grown trophozoites become paired as in Eugregarinina and encyst, in which condition they undergo sexual reproduction, followed by sporogony. Each individual which is now a gametocyte, produces gametes (*d-e*). Fusion of two gametes follows (*f*). The zygote develops into a spore containing 1-8 sporozoites (*g, a*).

One spore from 2 gametocytes.....Family 1 Ophryocystidae
Two or more spores from 2 gametocytes.....
.....Family 2 Schizocystidae (p. 411)

Family 1 **Ophryocystidae** Léger et Duboscq

Two gametocytes produce one spore; in Malpighian tubules of Coleoptera, gut of Ascidia and coelom of Oligochaeta.

Genus **Ophryocystis** Schneider. Schizogony by binary or multiple division; extracellular; schizonts conical, attached to host cells by pseudopods; a single spore in a pair of spheroidal gameto-

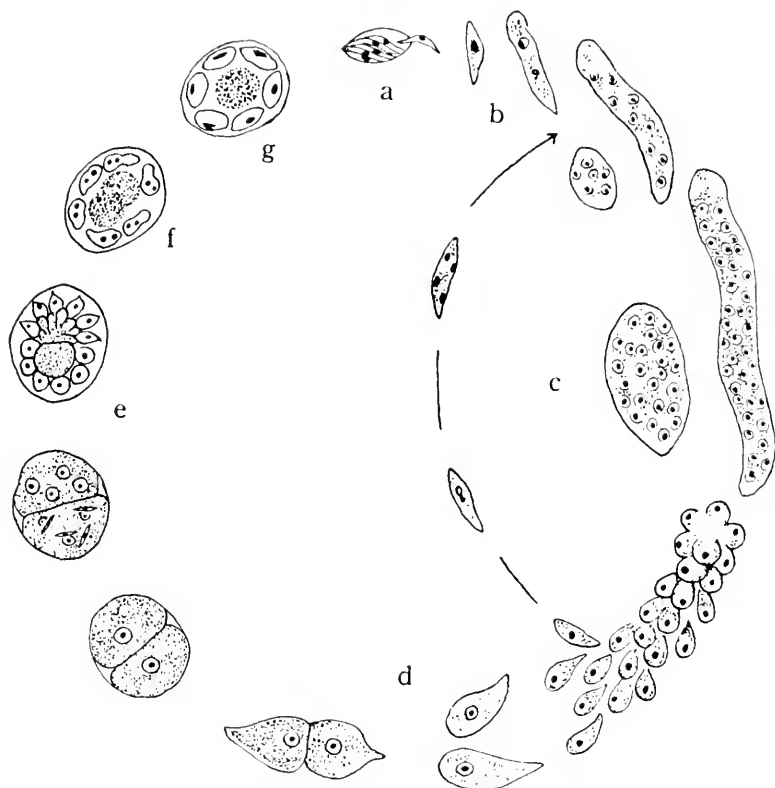


FIG. 185. The life-cycle of *Schizocystis gregarinoides*, $\times 1000$ (Léger). a, germinating spore; b, growth of schizonts; c, schizogony; d, two gametocytes and their association; e, stages in gamete formation, f, gametogony, g, cyst containing zygotes, each of which develops into a spore shown in a.

cytes; spore with 8 sporozoites; in Malpighian tubules of Coleoptera. Several species.

O. mesnili Léger (Fig. 186, a-e). In *Tenebrio molitor*; schizonts 1-4 nuclei; gametocytes 11μ in diameter; pairs $16-17\mu$ by 11μ ; spores biconical, 11μ by 7μ .

Genus **Merogregarina** Porter. Schizogony intracellular; trophozoites attached to gut epithelium by probosciform organelles; resembles somewhat *Selenidium*, but 2 gametocytes giving rise to one spore containing 8 sporozoites.

M. amaroucii P. (Fig. 186, f, g). In gut of the ascidian, *Ama-*

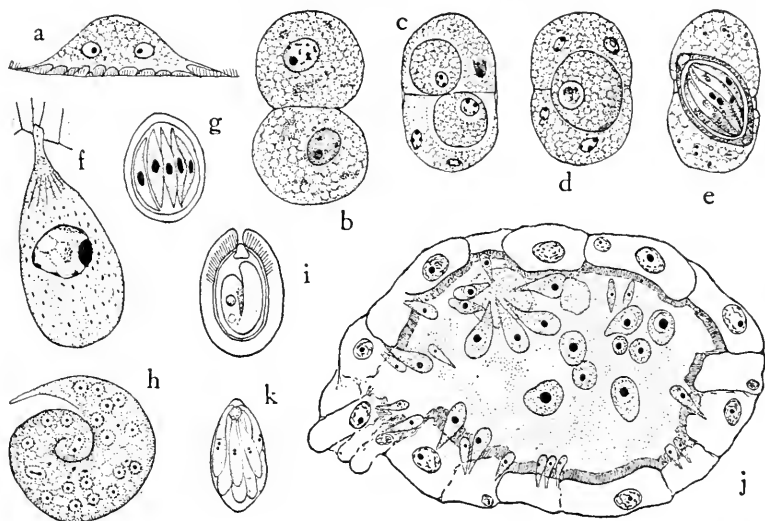


FIG. 186. a-e, *Ophryocystis mesnili* (a, trophozoite attached to Malpighian tubule; b-e, sporogony), $\times 1330$ (Léger); f, g, *Merogregarina amaroucii*, $\times 1000$ (Porter); h, i, *Spirocystis nidula* (h, $\times 770$; i, $\times 500$) (Léger and Duboseq); j, k, *Caulleryella pipientis* (j, gut of *Culex pipiens* with trophozoites, $\times 200$; k, a spore, $\times 1200$) (Buschkiel).

roucium sp.; extracellular; trophozoites with epimerite, $27-31\mu$ long; spore about 14μ long.

Genus **Spirocystis** Léger et Duboseq. Schizogony intracellular; schizonts curved, one end highly narrowed; mature schizonts snail-like, with numerous nuclei; repeated schizogony (?); gametes in chloragogen cells, somatic and visceral peritonium; association of 2 gametes produces a spore. One species.

S. nidula L. et D. (Fig. 186, h, i). In coelom and gut epithelium of *Lumbricus variegatus*; multinucleate schizonts about 35μ long; microgametes fusiform or ovoid, 7μ by 3μ ; macrogametes ovoid or spherical, 11μ in diameter; fusion of 2 gametes produces one spore which is thick-walled, 35μ long and contains one sporozoite, up to 40μ long.

Family 2 Schizocystidae Léger et Duboseq

Two or more spores are produced in a pair of gametocytes.

Genus **Schizocystis** Léger. Mature trophozoite multinucleate; ovoid or cylindrical with differentiated anterior end; schizogony by multiple division; trophozoites become associated, encyst, and

produce numerous (up to 30) spores, each with 8 sporozoites; in Diptera, Annelida, and Sipunculoida.

S. gregarinoides L. (Fig. 185). In gut of larvae of *Ceratopogon solstitialis*; mature schizonts up to 400μ by 15μ ; curved or spirally coiled; gametocytes $30\text{--}50\mu$ long; cysts ovoid, $16\text{--}32\mu$ long; spores biconical, 8μ by 4μ .

Genus **Syncystis** Schneider. Schizogony and sporogony extracellular; young trophozoites elongate, amoeboid; mature schizonts more or less spheroidal, producing some 150 merozoites; cysts spherical, producing about 150 spores. One species.

S. mirabilis S. (Fig. 187, *k, l*). In coelomic fluid and fat bodies of *Nepa cinerea*; merozoites, 7μ long; cysts spherical; spores navicular, 3–4 spines at ends, 10μ by 6μ , with 8 sporozoites (Steele).

Genus **Mattesia** Naville. Schizogony in the adipose tissue cell; 2 spores produced by a pair of gametocytes. One species.

M. dispora N. (Fig. 187, *m*). In adipose tissue cells of larvae of the flour moth, *Ephestia kuehniella* and *Plodia interpunctella* (pupa and adult also); schizonts $2.5\text{--}12\mu$ long; cyst $8\text{--}12\mu$ in diameter, with 2 spores, each with 8 sporozoites; spores 14μ by 7.5μ (Naville); 11μ by 6μ (maximum 13.5μ by 8μ) (Musgrave and Mackinnon). Highly pathogenic according to Musgrave and Mackinnon.

Genus **Caulleryella** Keilin. Schizogony extracellular; each gametocyte gives rise to 8 gametes, a pair forming 8 zygotes or spores; spore with 8 sporozoites; in gut of dipterous larvae. Several species.

C. pipientis Buschkiel (Fig. 186, *j, k*). Average trophozoites $50\text{--}60\mu$ by $23\text{--}26\mu$; with paraglycogen grains; schizogony produces 30–38 merozoites.

Genus **Lipotrophia** Keilin. Schizogony and sporogony intracellular; cyst contains 16 spores, each with 8 sporozoites; in fat body of *Systemus* larvae. One species.

L. macrospora K. (Fig. 187, *n*). Spores about 13.5μ by 3μ .

Genus **Selenidium** Giard. Schizogony intracellular; many spores produced by a pair of extracellular gametocytes; spore with 4 or more sporozoites; in gut of annelids.

S. potamillae Mackinnon et Ray (Fig. 187, *a–c*). Trophozoites euglenoid, average size 40μ by 15μ ; longitudinal striae; cysts oblong, producing many spores; spore, spherical with 4 (up to 10) sporozoites; in gut of the polychaete, *Potamilla reniformis*.

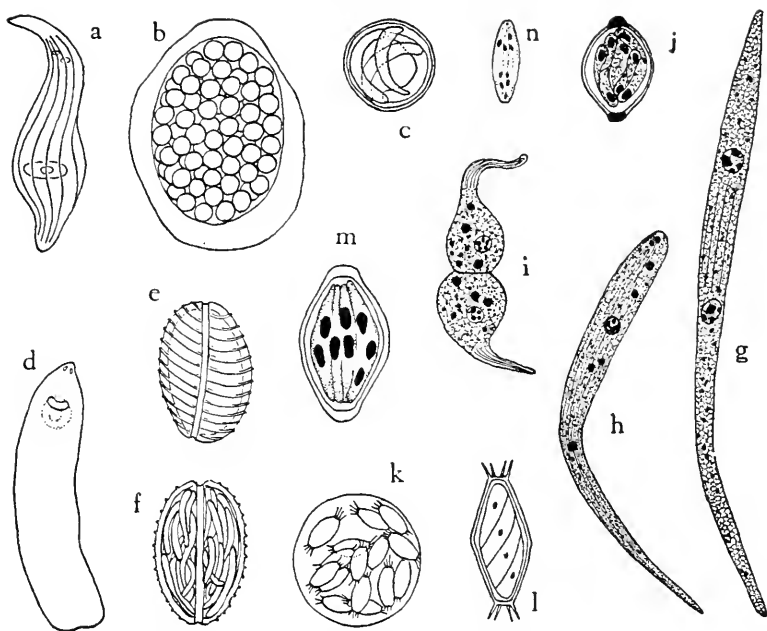


FIG. 187. a-c, *Selenidium potamillae* (a, $\times 420$; b, cyst with spores, $\times 330$; c, spore) (Mackinnon and Ray); d-f, *Meroselenidium keilini* (d, sporadin, $\times 670$; e, f, different views of spore, $\times 930$) (Mackinnon and Ray); g-j, *Machadoella triatomae* (g, a schizont, $\times 1420$; h, i, a single and associated gamonts, $\times 710$; j, spore, $\times 1920$) (Reichenow); k, l, *Syncystis mirabilis*: k, a cyst, $\times 470$ (Steopoe); l, spore (Schneider); m, *Mattesia dispora*, $\times 1480$ (Neville), n, *Lipotropha macrospora*, $\times 800$ (Keilin).

Genus **Meroselenidium** Mackinnon et Ray. Schizogony intracellular, initiated by formation of small masses which give rise to merozoites; about 20 spores from a pair of gametocytes; spores with numerous sporozoites. One species.

M. keilini M. et R. (Fig. 187, d-f). Large schizonts about 150μ by 30μ ; sporadins free in gut $200-300\mu$ by $40-70\mu$; paired gametocytes 85μ by 40μ ; spores $26-28\mu$ by $14-16\mu$, bivalve (?), transverse ridges, with many sporozoites; in gut of *Potomilla reniformis*.

Genus **Machadoella** Reichenow. Nematode-like, rigid; simple rounded anterior end; thick pellicle, longitudinally striated; schizogony in vermiform stage; head to head association of gametocytes; cysts with 3-6 spores, each with 8 sporozoites.

M. triatomae R. (Fig. 187, *g-j*). Schizonts about 55μ long; gametocytes $100-120\mu$ long; schizogony into 6-8 merozoites; cysts with 3-6 spores; spore $10-11\mu$ by $7-7.5\mu$; in Malpighian tubules of *Triatoma dimidiata*; Guatemala.

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CHAPTER 24

Order 2 **Coccidia** Leuckart

THE Coccidia show a wide zoological distribution, attacking the vertebrates and higher invertebrates alike. The majority are parasites of the epithelium of the digestive tract and its associated glands. Asexual reproduction is by schizogony and sexual reproduction by anisogamy in the majority of species. Both kinds of reproduction take place in one and the same host body, with the exception of such forms as *Aggregata* in which alternation of generations and of hosts occurs

Gametocytes similar; independent; a microgametocyte developing into many microgametes. Suborder 1 Eimeridea
Gametocytes dissimilar; association begins during the late trophic life; a few microgametes. Suborder 2 Adeleidea (p. 428)

Suborder 1 **Eimeridea** Léger

These Coccidia are, as a rule, intracellular parasites of the gut epithelium. Both asexual (schizogonic) and sexual (sporogonic) generations occur in one host, although in some there is also alternation of hosts. The life-cycle of *Eimeria schubergi*, a gut parasite of the centipede, *Lithobius forficatus*, as observed by Schaudinn, is as follows (Fig. 188). The infection begins when the mature oocysts of the coccidian gain entrance into the host through the mouth. The sporozoites escape from the spores and make their way through the micropyle of the oocyst into the gut lumen (*p*). By active movement they reach and enter the epithelial cells (*a*). These schizonts grow into large rounded bodies and their nuclei multiply in number. The newly formed nuclei move to the body surface, and each becomes surrounded by a small mass of cytoplasm, forming a merozoite. When the host cells rupture, the merozoites are set free in the gut lumen, make their way into new host cells and repeat the development (*b*). Instead of growing into schizonts, some merozoites transform themselves into macro- or micro-gametocytes (*c*). Each macrogametocyte contains refractile bodies, and becomes a mature macrogamete, after extruding part of its nuclear material (*d*, *e*). In the microgametocyte, the nucleus divides several times and each division-product assumes

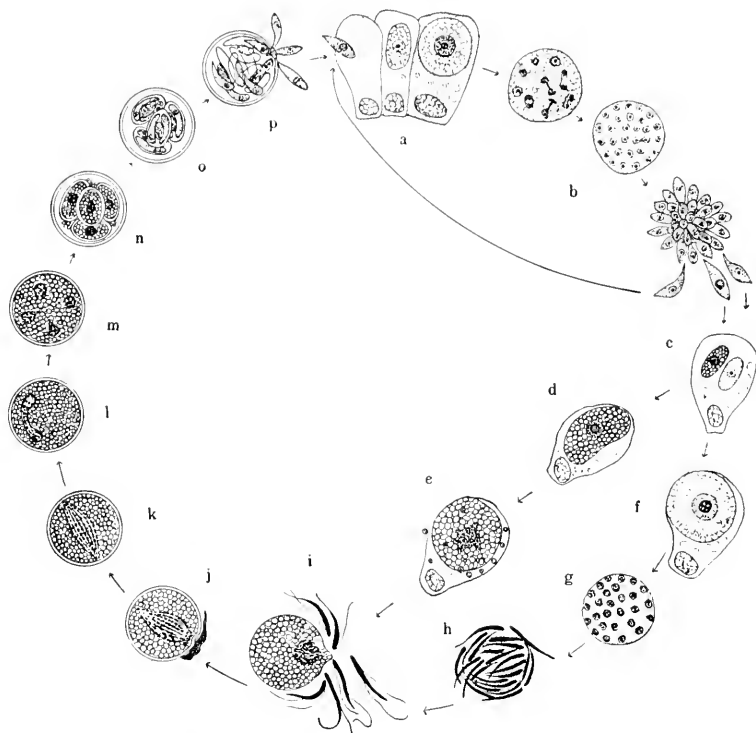


FIG. 188. The life-cycle of *Eimeria schubergi*, $\times 400$ (Schaudinn). a, entrance of a sporozoite in the gut epithelial cell of host and growth of schizont; b, schizogony; c, macro- and micro-gametocyte; d, e, formation of macrogamete; f-h, formation of microgametes; i, mature gametes prior to fusion; j, k, fertilization; l-n, spore-formation; o, oocyst containing four mature spores, each with two sporozoites; p, germination of spores in host's gut.

a compact appearance (f-h). The biflagellate comma-shaped microgametes thus produced, show activity when freed from the host cells (i). A microgamete and a macrogamete unite to form a zygote which secretes a membrane around itself (j). This stage is known as the **oocyst**. The nucleus divides twice and produces four nuclei (k-m). Each of the four nuclei becomes the center of a **sporoblast** which secretes a membrane and transforms itself into a **spore** (n). Its nucleus, in the meantime, undergoes a division, so that the two **sporozoites** become developed in the spore (o). Thus an oocyst of this species contains four spores and eight sporo-

zoites. Oocysts in the faecal matter become the sources of infection.

Body vermiform; schizogony in motile stage..... Family 1 Selenococcidiidae

Body not vermiform

Alternation of generations and of hosts..... Family 2 Aggregatidae

No alteration of hosts

Gametocytes associate early; many microgametes.....

..... Family 3 Dobelliidae (p. 421)

Gametocytes independent..... Family 4 Eimeriidae (p. 421)

Family 1 Selenococcidiidae Poche

Vermiform body and gametic differentiation place this family on the borderline between the Coccidia and Gregarinida.

Genus *Selenococcidium* Léger et Duboseq. Nucleus of vermiform trophozoite divides 3 times, producing 8 nuclei; trophozoite becomes rounded after entering gut-epithelium and divides into 8 schizonts; this is apparently repeated; schizonts develop into gametocytes; microgametocyte produces numerous microgametes; gametic union and sporogony (?). One species.

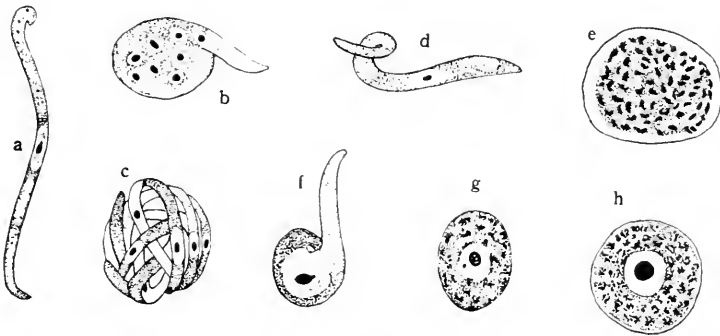


FIG. 189. *Selenococcidium intermedium*, $\times 550$ (Léger and Duboseq). a, schizont in host gut; b, c, schizogony; d, microgametocyte; e, microgametes; f, macrogametocyte; g, macrogamete; h, zygote (oocyst).

S. intermedium L. et D. (Fig. 189). Octonucleate vermiform schizont $60\text{--}100\mu$ long, and divides into vermicular merozoites in gut cells; parasitic in gut lumen of European lobster.

Family 2 Aggregatidae Labbé

Anisogamy results in production of zygotes which become transformed into many spores, each with 2-30 sporozoites; in

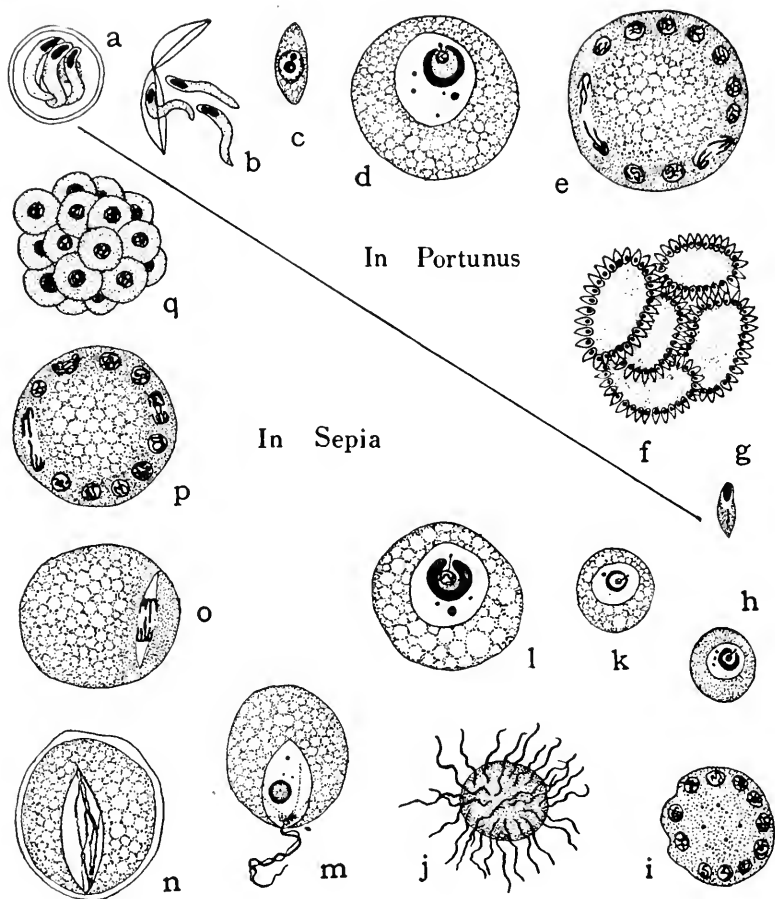


FIG. 190. The life-cycle of *Aggregata eberthi* (Dobell). a, a mature spore; b, germination of spore; c-f, schizogony; g, a merozoite, swallowed by *Sepia*; h-j, development of microgametes; k-l, development of macrogamete; m, fertilization; n, o, first zygotic division, chromosomes reduced in number from 12 to 6; p, q, development of sporoblasts, each of which develops into a spore with three sporozoites.

schizogony **cytomeres** first appear and then merozoites; alteration of generations and of hosts which are marine annelids, molluscs and crustaceans.

Genus **Aggregata** Frenzel. Schizogony in a crustacean and sporogony in a cephalopod; zygote produces many spores, each with 3 sporozoites. Many species.

A. eberthi (Labbé) (Fig. 190). Schizogony in *Portunus depurator* and sporogony in *Sepia officinalis*. Spores (*a*) germinate in the crab gut, each liberating 3 sporozoites (*b*) which grow and produce merozoites (10μ by 2μ) by schizogony in peri-intestinal connective tissue cells (6 chromosomes) (*c-f*); when host crab is eaten by a cuttlefish, merozoites penetrate gut wall and develop into micro- and macro-gametocytes (*h, k*), and further into gametes. (*j-l*); anisogamy (*m*) produces zygotes; zygote nucleus contains 12 chromosomes which become divided into 2 groups of 6 at first division (*n, o*); repeated nuclear division (*p*) forms many sporoblasts (*q*), each transforms itself into a spherical spore with 3 sporozoites (Dobell, Naville and Bělař).

Genus **Merocystis** Dakin. Sporogony in kidney of the whelk, *Buccinum*; schizogony unknown in another host (possibly a crab); microgametocytes produce first cytomeres which in turn form microgametes; anisogamy gives rise to zygotes, zygote forms many sporoblasts, each developing into a spore; spore spherical, with 2 sporozoites. One species.

M. kathae D. (Fig. 191, *a, b*). In kidney of *Buccinum undatum*; spores spherical, about 14μ in diameter.

Genus **Pseudoklossia** Léger et Duboseq. Anisogamy and sporogony in kidney of marine mussels; oocyst or zygote produces numerous spores; spore with 2 sporozoites; no residual body; schizogony unknown, in another host.

P. pectinis L. et D. (Fig. 191, *c*). In kidney of *Pecten maximus* in France; association of 2 sporozoites 3.5μ in diameter.

Genus **Caryotropha** Siedlecki. Both schizogony and sporogony take place in a host. One species.

C. mesnili S. In coelom (floating bundles of spermatogonia) of the polychaete, *Polymnia nebulosa*; schizogony in bundle of spermatogonia, in which cytomeres with 10–16 nuclei are formed and then merozoites; schizogony repeated; gametocytes undergo development also in the same host cells; macrogametes become set free in coelom, where union with microgametes takes place; each oocyst forms about 16 spores, spore with usually 12 sporozoites; cysts are extruded with reproductive cells of host worm.

Genus **Myriospora** Lermantoff. Anisogamy and sporogony in marine snails; schizogony unknown; oocyst forms numerous spores, each with 2 sporozoites. One species.

M. trophoniae L. In the cardiac body of polychaete, *Trophonia*

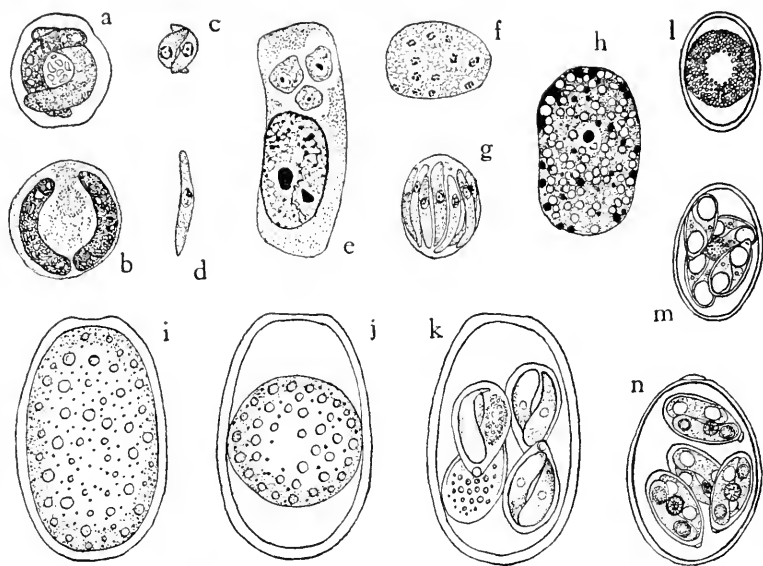


FIG. 191. a, b, *Merocystis kathae*, $\times 1000$ (Foulon); c, *Pseudoklossia pectinis*, two sporozoites of a spore, $\times 1470$ (Léger and Duboseq); d-k, *Eimeria stiedae*: d, a schizont; e, host cell with three schizonts; f, g, schizogony; h, macrogametocyte, $\times 1270$ (Hartmann); i-k, oocysts, $\times 830$ (Wasilewski); l, m, *E. perforans*, $\times 750$ (Pérard); n, *E. faurei*, $\times 800$ (Wenyon).

plumosa; macrogametes, vermiform, up to 800μ long, later ovoid; microgametocyte forms first about 100 cytomeres, each with some 20 nuclei; microgametes comma-shaped; anisogamy; oocyst with several hundred spores, each with about 24 sporozoites.

Genus **Hyaloklossia** Labbé. Schizogony unknown; sporogony in kidney of marine mussels; oocyst in organ-cavity; spherical spores of 2 kinds: smaller one with 2 spirally coiled sporozoites and the other with 4-6 sporozoites. One species.

H. pelseneeri Léger. Spherical oocysts $75-80\mu$ in diameter; spores 8μ and $11-12\mu$ in diameter; in kidney of *Tellina* sp. and *Donax* sp.

Genus **Angeiocystis** Brasil. Schizogony unknown; sporogony in polychaetes; oocyst forms 4 spores; spore oval, with about 30 sporozoites and residual body at a pole. One species.

A. audouinii B. In the cardiac body of *Audouinia tentaculata*; macrogametes vermiform, up to 65μ long.

Family 3 **Dobelliidae** Ikeda

Numerous microgametes develop from each microgametocyte; union of gametocytes begins early.

Genus **Dobellia** Ikeda. Schizonts sexually differentiated, microschizonts and macroschizonts; young schizonts binucleate; association of 2 gametocytes begins early as in *Adeleidea* (p. 428), but many microgametes are formed in each microgametocyte. One species.

D. binucleata I. In gut of *Petalostoma minutum*; mature oocyst 20–25 μ in diameter, with a thin wall, contains some 100 sporozoites without any spore membrane around them.

Family 4 **Eimeriidae** Léger

Macro- and micro-gametocytes develop independently; microgametocyte produces many gametes; an oocyst from a pair of anisogametes; oocyst with variable number of spores containing 1–many sporozoites, which condition is used as basis of generic differentiation. Oocysts as found in faeces of host are usually immature; time needed for completion of spore formation depends upon species, temperature, moisture, etc. Becker (1934) recommends the following bactericidal solutions in which oocyst may develop to maturity: 1% formaldehyde, 1% chromic acid or 2–4% potassium dichromate.

Genus **Eimeria** Schneider (*Coccidium* Leuckart). Zygote of oocyst develops 4 spores, each with 2 sporozoites. Numerous species.

E. schubergi (Schaudinn) (Fig. 188). In gut of *Lithobius forficatus*; oocysts spherical, 22–25 μ in diameter.

E. stiedae (Lindemann) (*Coccidium oviforme* Leuckart) (Fig. 191, *d–k*). In epithelium of bile-duct and liver (with white nodules) of rabbits; heavy infection is believed to be the cause of death of young animals, which may occur in an epidemic form; schizonts ovoid or spherical, 15–18 μ in diameter; merozoite 8–10 μ long; oocysts ovoid to ellipsoid, often yellowish, micropylar end flattened; mature oocysts 28–40 μ by 16–25 μ ; sporulation in 60–70 hours.

E. perforans Leuckart (Fig. 191, *l, m*). In gut of rabbits; pathogenic to host; oocysts with equally rounded ends, 24–30 μ by 14–20 μ ; sporulation in 30–48 hours.

E. zurni (Rivolta). In gut of cattle; said to be the cause of diar-

rhoea; oocysts spherical to ellipsoidal, $12\text{--}28\mu$ by $10\text{--}20\mu$; sporulation in 48–72 hours.

E. smithi Yakimoff et Galouzo. In gut of cattle; oocysts $25\text{--}32\mu$ by $20\text{--}29\mu$; sporulation in 3–5 days in shallow dishes, and 2 weeks in deep dishes (Becker).

E. ellipsoidalis Becker et Frye. In faeces of healthy calf; oocysts ellipsoidal, $20\text{--}26\mu$ by $13\text{--}17\mu$; sporulation in 18 days.

E. cylindrica Wilson. In faeces of cattle; oocysts cylindrical, $19\text{--}27\mu$ by $12\text{--}15\mu$; sporulation in 2–10 days.

E. faurei Moussu et Morotel (Fig. 191, *n*). In gut of sheep and goat; oocysts ovoid, $20\text{--}40\mu$ by $17\text{--}26\mu$; sporulation in 24–48 hours. Christensen (1938) recognized 7 species of *Eimeria* in the faeces of 100 North American sheep of which 96 contained oocysts.

E. arloingi Marotel. In gut of sheep and goat; oocysts with a cap, ovoid, $25\text{--}35\mu$ by $18\text{--}25\mu$; sporulation in 3 days.

E. intricata Spiegl. In gut of sheep and goat; oocysts with thick wall, with or without cap, ellipsoidal, $42\text{--}60\mu$ by $30\text{--}36\mu$; sporulation in about 9 days.

E. deblickei Douwes (Fig. 192, *a*). In gut of pigs; 30–82 per cent infection in California (Henry); oocysts $12\text{--}29\mu$ by $12\text{--}20\mu$; sporulation in 7–9 days.

E. scabra Henry. In caecal contents of pigs; oocysts, brown, ellipsoidal, $22\text{--}36\mu$ by $16\text{--}26\mu$. Henry (1931) recognized 2 other species in California swine.

E. caviae Sheather. In gut of guinea pigs; oocysts subspherical to ellipsoid, $13\text{--}26\mu$ by $13\text{--}22\mu$.

E. canis Wenyon (Fig. 192, *b*). In gut of dogs; oocysts, ellipsoidal, $18\text{--}45\mu$ by $11\text{--}28\mu$; spores 9.5μ by 2.5μ ; sporulation in 24 hours.

E. felina Nieschulz. In gut of cat; oocysts $21\text{--}26\mu$ by $13\text{--}17\mu$.

E. falciformis (Eimer) (Fig. 192, *c*). In gut of mice; oocysts spherical to ovoid, $16\text{--}21\mu$ by $11\text{--}17\mu$; sporulation in 3 days.

E. nieschulzi Dieben. In small intestine of rat; oocysts $16\text{--}26.4\mu$ by $13\text{--}21\mu$; sporulation in 65–72 hours.

E. separata Becker et Hall. In caecum and colon of rat; oocysts $13\text{--}19.5\mu$ by $11\text{--}17\mu$; sporulation in 27–36 hours.

E. miyairii Ohira. In small intestine of rat; oocysts $16.5\text{--}29\mu$ by $16\text{--}26\mu$; sporulation in 96–120 hours.

E. tenella (Railliet et Lucet) (Fig. 192, *d*). In caecum, colon and lower small intestine of chicken; cause of acute coccidiosis (Tyzzer); in caecal contents of California quail (Henry); schizogony in

caecum; oocysts $19.5\text{--}26\mu$ by $16.5\text{--}23\mu$; sporulation in 48 hours; heavily infected caecum highly haemorrhagic.

E. mitis Tyzzer (Fig. 192, e). In anterior region of small in-

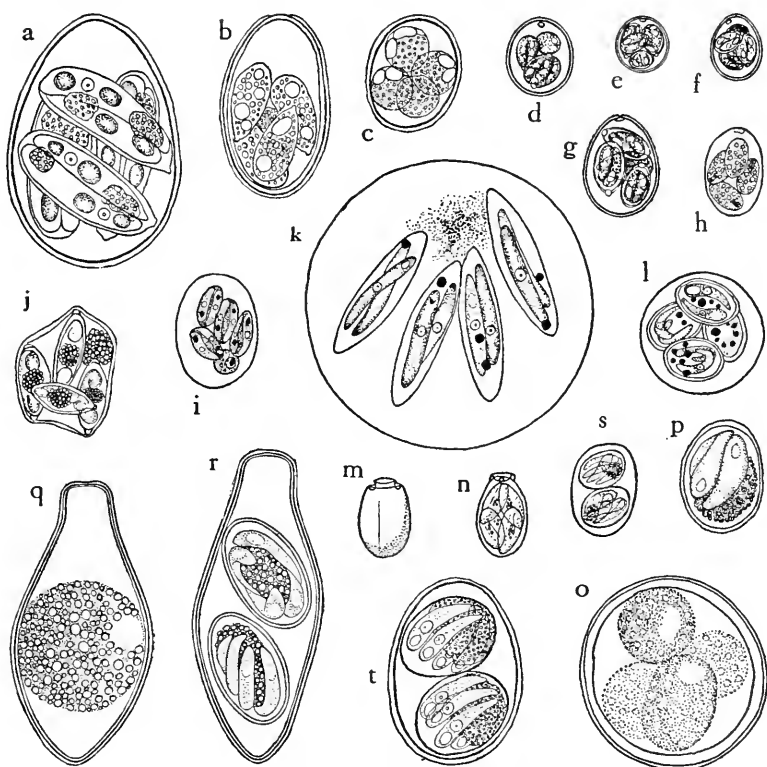


FIG. 192. a, *Eimeria deblickei*, $\times 1070$ (Wenyon); b, *E. canis*, $\times 650$ (Wenyon); c, *E. falciformis*, $\times 730$ (Wenyon); d, *E. tenella*, $\times 600$ (Tyzzer); e, *E. mitis*, $\times 430$ (Tyzzer); f, *E. acervulina*, $\times 430$ (Tyzzer); g, *E. maxima*, $\times 470$ (Tyzzer); h, *E. ranarum*, $\times 670$ (Laveran and Mesnil); i, *E. prevoti*, $\times 670$ (Laveran and Mesnil); j, *E. ranae*, $\times 670$ (Dobell); k, *E. sardinae*, $\times 600$ (Thomson and Robertson); l, *E. clupearum*, $\times 600$ (Thomson and Robertson); m, n, *Jarrina paludosa*, $\times 800$ (Léger and Hesse); o, p, *Wenyonella africana*, $\times 1330$ (Hoare); q, r, *Isospora hominis*, $\times 1400$ (Dobell); s, *I. bigemina*, $\times 930$ (Wenyon); t, *I. rivolta*, $\times 930$ (Wenyon).

testine of chicken; oocysts subspherical, 16.2μ by 15.5μ ; sporulation in 48 hours.

E. acervulina T. (Fig. 192, f). In anterior region of small intestine of chicken; also in California quail (Henry); oocysts oval,

17.7–20.2 μ by 13.7–16.3 μ ; sporulation in 20 hours; associated with serious chronic coccidiosis (Tyzzer).

E. maxima T. (Fig. 192, *g*). In mid-gut of chicken; oocysts oval, 21.5–42.5 μ by 16.5–29.8 μ .

E. necatrix Johnson. In small intestine (schizonts) and caecum (oocysts) of chicken; cause of chronic coccidiosis; oocysts obovate, 13–23 μ by 11–18 μ ; sporulation in 48 hours.

E. praecox J. In the upper third of small intestine of chicken; oocysts ovoid, 20–25 μ by 15.5–20 μ ; sporulation in 48 hours.

E. meleagridis Tyzzer. In caecum of turkey; apparently non-pathogenic; oocysts, ellipsoidal, 19–30 μ by 14.5–23 μ .

E. meleagritidis T. In lower small intestine in turkey; somewhat similar to *E. mitis*; oocysts, 16.5–20.5 μ by 13.2–17.2 μ .

E. truncata (Railliet et Lueet). In kidney of geese; oocysts truncate at one pole, ovoid, 14–23 μ by 13–18 μ ; some observers find that this coccidian is fatal to young geese.

E. anseris Kotlan. In gut of geese; oocysts spherical or pyriform, 11–16 μ in diameter.

E. labbeana Pinto. In gut of domestic pigeon; oocysts sometimes light brown, 15–26 μ by 14–24 μ .

E. dispersa Tyzzer. In small intestine of bob-white quail and pheasant; oocysts ovate, 18.8–22.8 μ (quail), smaller in pheasant, without polar inclusion; sporulation in about 24 hours.

E. ranarum (Labbé) (Fig. 192, *h*). In gut epithelium (nuclei) of frogs; oocysts about 17 μ by 12 μ .

E. prevoti (Laveran et Mesnil) (Fig. 192, *i*). In gut epithelium of frogs; oocysts about 17 μ by 12 μ ; when sporozoites are fully formed, the spore membranes dissolve.

E. ranae Dobell (Fig. 192, *j*). In gut of frogs; oocysts 22 μ by 18 μ .

E. sardinae (Thélohan) (*E. oxyspora* Dobell) (Fig. 192, *k*). In testis of sardine; oocysts spherical 30–50 μ .

E. clupearum (Thélohan) (*E. wenyoni* Dobell) (Fig. 192, *l*). In liver of herrings, mackerels, and sprats; oocysts, spherical, 18–33 μ in diameter.

E. gadi Fiebiger. In swim-bladder of *Gadus virens*, *G. morrhua*, and *G. aeglefinus*; schizogony and sporogony; germination of spores takes place in the bladder of the same host individual, bringing about a very heavy infection; oocysts 26–28 μ ; pathogenic (Fiebiger).

Genus **Jarrina** Léger et Hesse. Oocysts ovoid, one end rounded

and the other drawn out into a short neck; 4 spores, each with 2 sporozoites.

J. paludosa L. et H. (Fig. 192, *m, n*). In gut of *Fulica atra* and *Gallinula chloropus*; oocysts 15μ by 11μ ; sporulation in 15 days.

Genus **Wenyonella** Hoare. Oocysts with 4 spores, each with 4 sporozoites. One species.

W. africana H. (Fig. 192, *o, p*). In small intestine of *Boaedon lineatus* ("brown snake") in Uganda; oocysts ovoid or subspherical, 18.5 – 19.2μ by 16 – 17.6μ ; spores ovoid, 9.6μ by 8μ ; sporulation in 5–6 days.

Genus **Isospora** Schneider. Oocyst produces 2 spores, each containing 4 sporozoites.

I. hominis (Railliet et Lucet) (*I. belli* Wenyon) (Fig. 192, *q, r*). In human small intestine; oocysts 25 – 33μ by 12.5 – 16μ ; spores 12 – 14μ by 7 – 9μ ; in one case of accidental infection, the victim suffered 6 days later diarrhoea with abdominal discomfort which lasted for 4 weeks, and recovered.

I. bigemina (Stiles) (Fig. 192, *s*). In gut of cat and dog; oocysts 10 – 14μ by 7 – 9μ .

I. rivolta (Grassi) (Fig. 192, *t*). In gut of cat and dogs; oocysts 20 – 25μ by 15 – 20μ .

I. felis Wenyon (Fig. 193, *a*). In cat and dog; oocysts 39 – 48μ by 26 – 37μ .

I. suis Biester. In swine faeces; oocysts subspherical, about 22.5μ by 19.4μ ; sporulation in 4 days.

I. lacazei Labbé. In small intestine of passerine birds (sparrows, blackbirds, finches, etc.); oocysts subspherical, 18.5 – 30μ by 18 – 29.2μ ; heavily infected sparrow shows definite symptoms; sporulation in 4–5 days.

I. lieberkuhni (Labbé) (Fig. 193, *b*). Oocyst about 40μ long; in kidney of frogs.

Genus **Cyclospora** Schneider. Development similar to that of *Eimeria*; oocyst with 2 spores, each with 2 sporozoites and covered by a bi-valve shell.

C. caryolytica Schaudinn (Fig. 193, *c*). In gut of mole; sporozoites enter and develop in the nuclei of gut epithelial cells; oocyst oval, about 15μ by 11.5μ .

Genus **Dorisiella** Ray. Zygote develops (without becoming oocyst) into 2 spores, each with 8 sporozoites; macrogametocytes migratory.

D. scolelepidis R. (Fig. 193, d). In gut of *Scolecopsis fuliginosa*; zygote contents divide into 2 oval spores, 12–16 μ by 6–10 μ ; spore with 8 sporozoites.

Genus **Caryospora** Léger Oocyst develops into a single spore

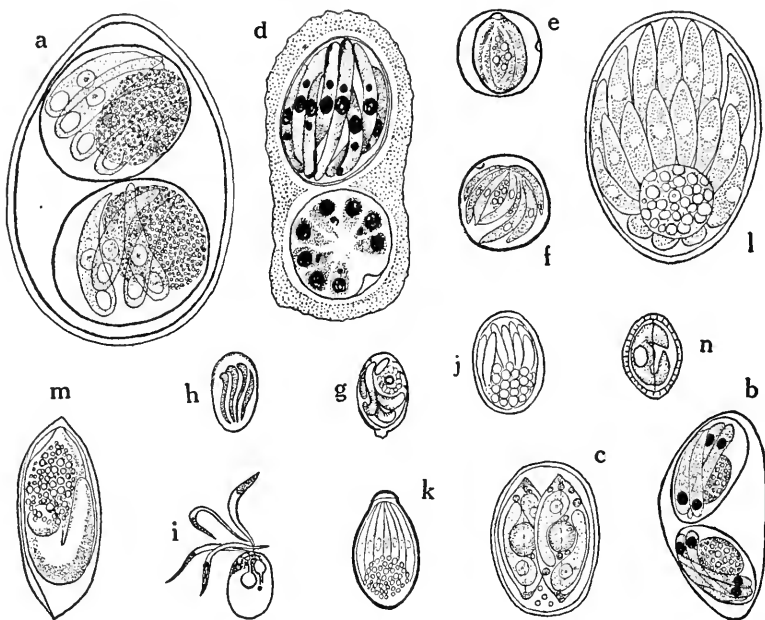


FIG. 193. a, *Isospora felis*, $\times 930$ (Wenyon); b, *I. lieberkuhni*, $\times 660$ (Laveran and Mesnil); c, *Cyclospora caryolytica*, $\times 1330$ (Schaudinn); d, *Dorisiella scolelepidis*, oocyst with two spores, $\times 1400$ (Ray); e, f, *Caryospora simplex*, $\times 800$ (Léger); g–i, *Cryptosporidium muris* (g, h, oocysts; i, emergence of four sporozoites), $\times 1030$ (Tyzzer); j, *Pfeifferinella ellipsoides*, $\times 1330$ (Wasielewski); k, *P. impudica*, $\times 800$ (Léger and Hollande); l, *Lankesterella minima*, a mature cyst in endothelial cell, $\times 1000$ (Nöller); m, *Barrouxia ornata*, $\times 1330$ (Schneider); n, *Echinosporea labbei*, $\times 1000$ (Léger).

with 8 sporozoites and a residual mass; membrane thick and yellow. One species.

C. simplex L. (Fig. 193, e, f). In gut-epithelium of *Vipera aspis*; oocyst thick-walled, 10–15 μ in diameter.

Genus **Cryptosporidium** Tyzzer. Lumen-dwelling minute organisms; oocyst with 4 sporozoites.

C. muris T. (Fig. 193, g–i). In peptic glands of the mouse; both

schizogony and sporogony in the mucoid material on surface of the epithelium; oocysts 7μ by 5μ ; 4 sporozoites, $12-14\mu$ long.

C. parvum T. In glands of small intestine of the mouse; oocysts with 4 sporozoites, 4.5μ in diameter.

Genus **Pfeifferinella** Wasielewski. Macrogamete with a "reception tubule" by which microgametes enter; oocyst produces directly 8 sporozoites.

P. ellipsoides W. (Fig. 193, *j*). In liver of *Planorbis corneus*; oocysts oval, $13-15\mu$ long.

P. impudica Léger et Hollande (Fig. 193, *k*). In liver of *Limax marginatus*; oocysts ovoid, 20μ by 10μ .

Genus **Lankesterella** Labbé. Oocyst produces 32 or more sporozoites directly without spore-formation; in endothelial cells of cold-blooded vertebrates; mature sporozoites enter erythrocytes in which they are transmitted to a new host individual by blood-sucking invertebrates.

L. minima (Chaussat) (Fig. 193, *l*). In frogs; transmitted by leeches (*Placobdella marginata*); frog acquires infection through introduction of sporozoites by leech; sporozoites make their way into the blood capillaries of various organs; there they enter endothelial cells; schizogony produces numerous merozoites which bring about infection of many host cells; finally macro- and micro-gametocytes are formed; anisogamy produces zygotes which transform into oocysts, in which a number of sporozoites develop; these sporozoites are set free upon disintegration of cyst wall in the blood plasma and enter erythrocytes (Nöller); oocyst oval, about 33μ by 23μ .

Genus **Schellackia** Reichenow. Oocyst spherical with 8 sporozoites, without spore membrane; in gut of lizards.

S. bolivari R. In mid-gut of *Acanthodactylus vulgaris* and *Psammodromus hispanicus*; development similar to *Eimeria schubergi* (Fig. 188); oocysts, spherical, $15-19\mu$ in diameter, with 8 sporozoites.

Genus **Barrouxia** Schneider. Oocyst with numerous spores, each with a single sporozoite; spore membrane uni- or bi-valve, with or without caudal prolongation.

B. ornata S. (Fig. 193, *m*). In gut of *Nepa cinerea*; oocysts spherical, $34-37\mu$ in diameter, with many spores; spore with one sporozoite and bivalve shell, $17-20\mu$ by $7-10\mu$.

Genus **Echinospira** Léger. Oocyst with 4-8 spores, each with a

sporozoite; endospore with many small spinous projections.

E. labbei L. (Fig. 193, *n*). In gut of *Lithobius mutabilis*; oocyst spherical, 30–40 μ in diameter; spores, 11 μ by 9.4 μ , with bi-valve shell; sporulation completed in about 20 days.

Suborder 2 Adeleidea Léger

The Adeleidea are on the whole similar to Eimeridea in their habitat and development, but the micro- and macro-gametocytes become attached to each other in pairs during the course of development into gametes (Fig. 194), and each microgametocyte produces a few microgametes. The zygote becomes oocyst which produces numerous sporoblasts, each of which develops into a spore with 2 or 4 sporozoites.

In epithelium of gut and its appended glands of chiefly invertebrates.

..... Family 1 Adeleidae

In cells of circulatory system of vertebrates.....

..... Family 2 Haemogregarinidae (p. 431)

Family 1 Adeleidae Léger

Genus **Adelea** Schneider. Zygote develops into a thinly walled oocyst with numerous flattened spores, each with 2 sporozoites; in arthropods.

A. ovata S. (Fig. 194). In gut of *Lithobius forficatus*; merozoites 17–22 μ long; spores 11–14 μ in diameter by 6 μ thick; sporozoites 20 μ by 4 μ .

Genus **Adelina** Hesse. Oocyst thick-walled; spores spherical, comparatively small in number; in gut or coelom of arthropods and oligochaetes.

A. dimidiata (Schneider) (Fig. 195, *a*). In gut of *Scolopendra cingulata* and other myriapods; oocysts with 3–17 spores.

A. octospora H. (Fig. 195, *b*). Spherical oocyst contains 8 spores, in coelom of *Slavina appendiculata*.

Genus **Klossia** Schneider. Oocyst with numerous spherical spores, each with 3–10 sporozoites. Several species.

K. helicina S. In kidneys of various land-snails, belonging to genera *Helix*, *Succinea*, and *Vitrina*; oocyst with a double envelope 120–180 μ in diameter; spores 12 μ in diameter, with 5–6 sporozoites.

Genus **Orcheobius** Schuberg et Kunze. Macrogametes vermiform; oocyst with 25–30 spores, each with 4 (or 6) sporozoites.

O. herpobdellae S. et K. (Fig. 195, *c*). In testis of *Herpobdella*

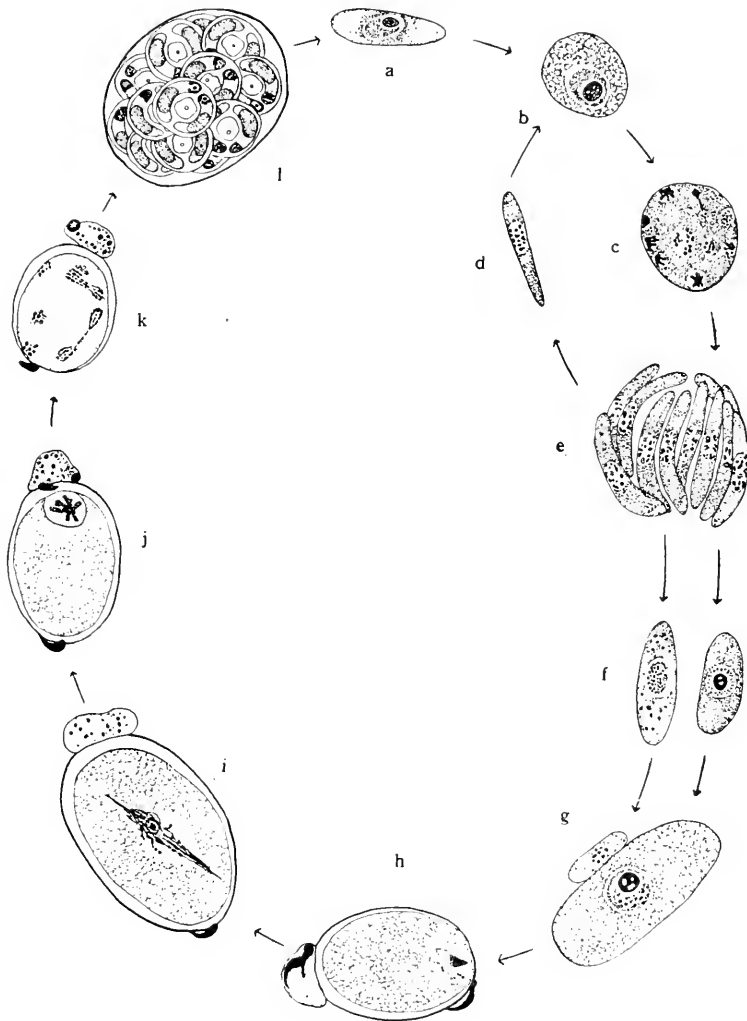


FIG. 194. The life-cycle of *Adelea ovata*, $\times 600$ (Schellack and Reichenow). a, schizont which enters the gut epithelium of the host centipede; b-d, schizogony; e, larger forms of merozoites; f, microgametocyte (left) and macrogametocyte (right); g, association of gametocytes; h, i, fertilization; j, zygote; k, nuclear division in zygote; l, mature oocyst with numerous spores.

atomaria; mature macrogametes 180μ by 30μ ; microgametes 50μ by 12μ ; schizogony in April and May; sporogony in June and July.

Genus **Klossiella** Smith et Johnson. Microgametocyte produces

2 microgametes; oocyst with many spores, each with numerous sporozoites; in kidney of mammals.

K. muris S. et J. (Fig. 195, d, e). Oocyst with 12–16 spores; spore with about 25 sporozoites, discharged in urine; in kidney of mouse.

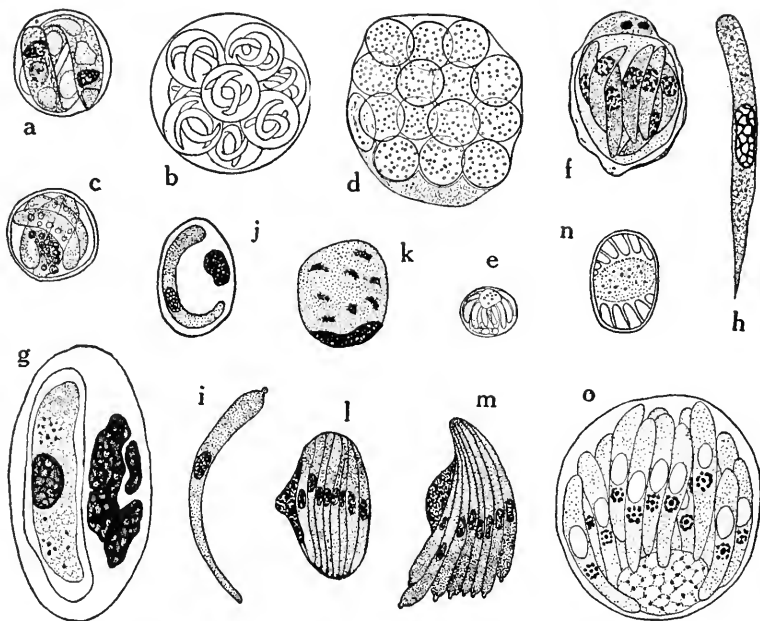


Fig. 195. a, *Adelina dimidiata*, spore, $\times 1000$ (Schellack); b, *A. octospora*, oocyst, $\times 1000$ (Hesse); c, *Orcheobius herpobdellae*, $\times 550$ (Kunze); d, e, *Klossiella muris* (d, renal cell of host with 14 sporoblasts; e, spore), $\times 280$ (Smith and Johnson); f, *Legerella hydropori*, oocyst, $\times 1000$ (Vincent); g, h, *Haemogregarina* of frog, $\times 1400$ (Kudo); i–m, *H. simondi*, in the blood of the sole, *Soleu vulgaris*, $\times 1300$ (Laveran and Mesnil); n, *Hepatozoon muris*, spore, $\times 420$ (Miller); o, *Karyolysus lacertarum*, $\times 700$ (Reichenow).

K. cobayae Seidelin. Oocyst with 8–20 spores; spore with about 30 sporozoites; in kidney of guinea pig.

Genus **Legerella** Mesnil. Oocyst contains numerous sporozoites; spores entirely lacking; in arthropods.

L. hydropori Vincent (Fig. 195, f). In epithelium of Malpighian tubules of *Hydroporus palustris*; oocysts ovoid, $20\text{--}25\mu$ long, with 16 sporozoites which measure 17μ by 3μ .

Genus **Chagasella** Machado. Oocyst with 3 spores, each with 4 or 6 (or more) sporozoites; in hemipterous insects.

C. hartmanni (Chagas). In gut of *Dysdercus ruficollis*; oocysts with 3 spores about 45μ in diameter; spore with 4 sporozoites, about 35μ by 15μ .

Family 2 **Haemogregarinidae** Léger

With 2 hosts: vertebrates (circulatory system) and invertebrates (digestive system).

Genus **Haemogregarina** Danilewsky. Schizogony takes place in blood cells of vertebrates; merozoites develop into gametocytes; when taken into gut of leech or other blood-sucking invertebrates, sexual reproduction takes place; microgametocyte develops 2 or 4 microgametes; sporozoites formed without production of spores.

H. stepanowi D. (Fig. 196). Schizogony in *Emys orbicularis* and sexual reproduction in *Placobdella catenigera*; sporozoites introduced into blood of the chelonian host by leech (*a*), and enter erythrocytes in which they grow (*d-g*); schizogony in bone-marrow, each schizont producing 12-24 merozoites (*h*); schizogony repeated (*i*); some merozoites produce only 6 merozoites (*j*, *k*) which become gametocytes (*l-o*); gametogony occurs in leech; 4 microgametes formed from each microgametocyte and become associated with macrogametocytes in gut of leech (*p-r*); zygote (*s*) divides three times, and develops into 8 sporozoites (*t-w*).

Haemogregarina are commonly found in various frogs (Fig. 195, *g*, *h*) and in fishes (Fig. 195, *i-m*).

Genus **Hepatozoon** Miller. Schizogony in cells of liver, spleen, and other organs of vertebrates; merozoites enter erythrocytes or leucocytes and develop into gametocytes; in blood-sucking arthropods (ticks, mites), micro- and macrogametes develop and unite in pairs; zygotes become oocysts which increase in size and produce sporoblasts, spores, and sporozoites.

H. muris (Balfour) (Fig. 195, *n*). In various species of rat; several specific names were proposed on the basis of difference in host, locality, and effect on the host, but they are so indistinctly defined that specific separation appears to be impossible. Schizogony in liver of rat; young gametocytes invade mononuclear leucocytes and appear as haemogregarines; when blood is taken in by the mite, *Laelaps echidninus*, union of 2 gametes produces

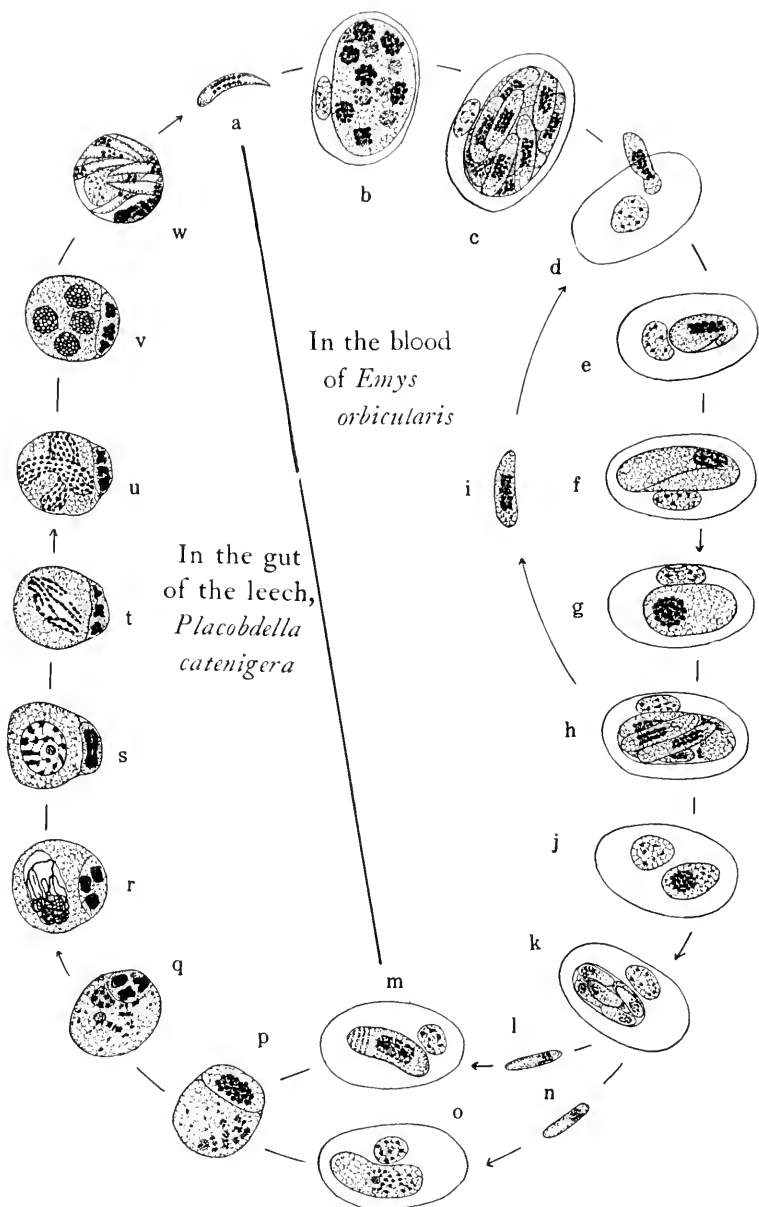


FIG. 196. The life-cycle of *Haemogregarina stepanowi*, $\times 1200$ (Reichenow). a, sporozoite; b-i, schizogony; j-k, gametocyte-formation; l, m, microgametocytes; n, o, macrogametocytes; p, q, association of gametocytes; r, fertilization; s-w, division of the zygote nucleus to form eight sporozoites.

vermicular body which penetrates gut-epithelium and reaches peri-intestinal tissues and grows; becoming surrounded by a cyst-membrane, cyst contents break up into a number of sporoblasts and then into spores, each of which contains a number of sporozoites; when a rat devours infected mites, it becomes infected.

Genus **Karyolysus** Labbé. Sporoblasts formed in oocysts in gut-epithelium of mite, vermiform sporokinets, enter host ova and become mature; when young mites hatch, spores in gut-epithelium are cast off and discharged in faeces; a lizard swallows spores; liberated sporozoites enter endothelial cells in which schizogony takes place; merozoites enter erythrocytes as gametocytes which when eaten by a mite complete development in its gut.

K. lacertarum (Danilewsky) (Fig. 195, o). In *Lacerta muralis*; sexual reproduction in *Liponyssus saurorum*; sporokinets 40–50 μ long; spores 20–25 μ in diameter.

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Order 3 Haemosporidia Danilewsky

THE development of the Haemosporidia is, on the whole, similar to that of the Coccidia in that they undergo asexual reproduction, or schizogony, and also sexual reproduction, or sporozoite-formation; but the former takes place in the blood of vertebrates and the latter in the alimentary canal of some blood-sucking invertebrates. Thus one sees that the Haemosporidia remain always within the body of one of the two hosts; hence, the sporozoites do not possess any protective envelope.

The Haemosporidia are minute intracorpuseular parasites of vertebrates. The malarial parasites of man are typical members of this order. The development of *Plasmodium vivax* is as follows (Fig. 197): Infected anopheline mosquitoes introduce the **sporozoites** (*a*) which invade the **erythrocytes** (*b*), grow, and undergo schizogony, forming a number of **merozoites** (*c-f*). The latter upon liberation from the host cells, attack other erythrocytes. Some of the merozoites develop into **macrogametocytes** (*g*) and others, **microgametocytes** (*i, j*). No further changes ordinarily take place in the human body, but the schizogony is repeated. The protozoan produces **melanin** (or haemozoin) which is apparently the metabolic product of the organism at the expense of the haemoglobin. When the blood is taken into the stomach of a suitable species of anopheline mosquito, the gametocytes develop into **macrogametes** and **microgametes** respectively (*h, k*). They unite in pairs (*l*) and thus **ookinetes** (zygotes) (*m*) are formed. The ookinetes penetrate the stomach wall and become lodged between the epithelium and the elastic membrane of the stomach (*n*). There they grow and the nuclei undergo rapid and repeated divisions, finally producing an enormous number of minute sporozoites (*o, p*). These sporozoites are set free through the rupture of the cyst wall in the body cavity, find their way into the salivary glands and wait for an opportunity of being inoculated into a new victim (*q*). The schizogony occurs regularly, and it is thought that the typical malarial fever is caused by some toxic substances which are liberated into the blood stream when innumerable merozoites become set free in the latter.

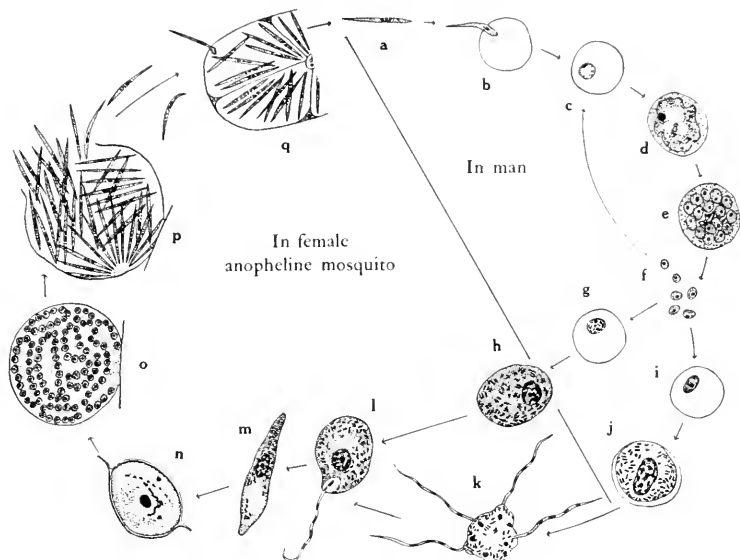


FIG. 197. The life-cycle of *Plasmodium vivax* (various authors). a, sporozoite entering human blood plasma; b, sporozoite entering erythrocyte; c, young schizont; d-f, schizogony; g, h, macrogametocytes; i, j, microgametocytes; k, microgametes formed in the stomach of mosquito; l, union of gametes; m, zygote or ookinete, penetrating through the gut wall; n, rounding up of an ookinete between the gut wall and elastic membrane; o, oocyst in which sporozoites are being developed; p, mature oocyst ruptured and the sporozoites are set free in the body fluid; q, sporozoites entering the salivary gland.

With pigment granules

Schizogony in peripheral blood of vertebrates.....

.....Family 1 Plasmodiidae

Gametocytes in peripheral blood; schizogony elsewhere.....

.....Family 2 Haemoproteidae (p. 439)

Without pigment granules; minute parasites of erythrocytes.....

.....Family 3 Babesiidae (p. 442)

Family 1 Plasmodiidae Mesnil

Genus **Plasmodium** Marchiafava et Celli. Schizogony in erythrocytes of vertebrates; anisogamy and sporozoite-formation in Anopheles or Culex mosquitoes; widely distributed. Numerous species.

P. vivax (Grassi et Feletti) (Fig. 198, a-g). The organism of benign tertian malaria of man; schizogony completed in 48 hours;

infected erythrocytes become enlarged, widely distributed over temperate and tropical countries.

P. falciparum (Welch) (Fig. 198, *h-n*). The organism of malignant tertian, subtertian, or aestivo-autumnal malaria of man, schizogony completed in 24-48 hours; schizonts adhere to capillary wall, to which malignancy of the species is attributed; gametocytes crescentic (some authors therefore place this species in genus *Laverania*); of more limited distribution in tropical and subtropical regions of the world.

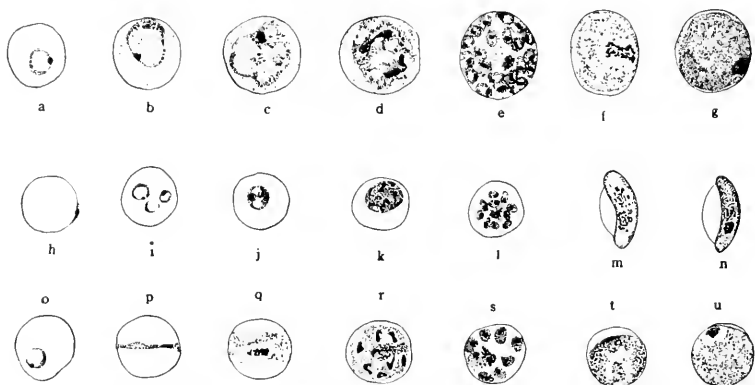


FIG. 198. a-g, *Plasmodium vivax*, $\times 1000$ (Kudo); h-n, *P. falciparum*, $\times 1000$ (Kudo); o-u, *P. malariae*, $\times 1000$ (Kudo). a-e, h-l, o-s, schizogony; f, m, t, microgametocytes; g, n, u, macrogametocytes.

P. malariae (Laveran) (Fig. 198, *o-u*). The organism of quartan malaria of man; schizogony completed in 72 hours; in tropical and subtropical countries.

Numerous species of female mosquitoes belonging to the genus *Anopheles* transmit these organisms. In the United States, the chief species concerned is *A. quadrimaculatus*.

The malaria parasites are usually studied in (Giemsa, Wright, or Hasting) stained blood films or smears; the comparison of the three species of human malaria given on the following page is based upon observations of stained specimens.

A number of species of *Plasmodium* have been reported from various avian hosts. Manwell (1935) recognizes the following species as occurring in the United States. Hegner and his colleagues (1938) have called attention to the fact that merozoites enter young red corpuscles or reticulocytes (Fig. 199, *f, g*).

	<i>P. vivax</i>	<i>P. falciparum</i>	<i>P. malariae</i>
Schizogony completed in	48 hours	24-48 hours	72 hours
Diameter of ring form	$\frac{1}{3}$ - $\frac{1}{2}$ of erythrocyte	$\frac{1}{6}$ of erythrocyte, delicate	$\frac{1}{3}$ - $\frac{1}{2}$ of erythrocyte
Size of infected cell	larger than uninfected one; paler	same as uninfected one	same as uninfected one; distorted
Dots in infected cell	Schüffner's dots	Maurer's dots	not seen
Grown schizonts	amoeboid, large	round, small	elongate oval, medium
Pigment granules in organism	rod-shaped	small triangular	large, irregular
Number of merozoites from a schizont	15 or more	about 8-10 or more	8-10
Merozoites arranged in erythrocyte	in 2 rings or scattered	2 rings or scattered	one ring
Gametocytes	rounded	crescentic	rounded

P. praecox (Grassi et Feletti) (Fig. 199, *a-e*). In English and Spanish sparrows; schizogony completed in 30-36 hours; number of merozoites from a single schizont 8-15; gametocytes crescentic; pigments occur in both schizonts and gametocytes; sexual cycle takes place in female culicine mosquitoes; organism maintains its characteristics when inoculated into canaries, *Serinus canaria*.

P. cathemerium Hartman (Fig. 199, *f-l*). In sparrows, cowbirds, and red-winged blackbirds; schizogony completed in 24 hours; number of merozoites 6-24; gametocytes spherical, with rod-shaped pigment granules; pigment granules in microgametocytes longer and more pointed than those in macrogametocytes; macrogametocytes usually stain more deeply, schizonts without vacuoles; pigments in schizonts amorphous mass; merozoites 1μ long; mature schizonts and gametocytes 7-8 μ in diameter; transmitted by, or sexual reproduction in, *Culex pipiens*, *C. salinarius*, *C. ter-*

ritans, *C. quinquefasciatus*, *C. tarsalis*, *Aedes aegypti* and *A. sollicitans*.

P. elongatum Huff (Fig. 199, *m-p*). In English sparrows and canaries; merozoites 8-12; round pigment granules clumped in schizonts, scattered in gametocytes; gametocytes elongate; schi-

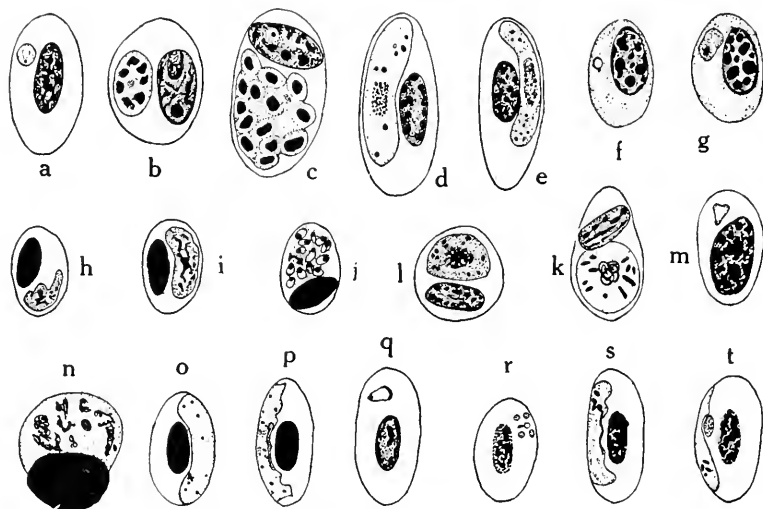


FIG. 199. a-e, *Plasmodium praecox* (a-c, schizogony; d, microgametocyte; e, macrogametocyte), $\times 1670$ (Hartman); f-l, *P. cathemerium* (f-j, schizogony, $\times 1100$ (Hegner and Hewitt); k, microgametocyte; l, macrogametocyte, $\times 1670$ (Hartman)); m-p, *P. elongatum* (m, n, schizonts; o, microgametocyte; p, macrogametocyte), $\times 1330$ (Manwell); q-t, *P. vaughni* (q, r, schizonts; s, microgametocyte; t, macrogametocyte), $\times 1330$ (Manwell).

zogony usually in erythrocytes of bone marrow; gametocytes numerous in peripheral blood.

P. vaughni (Novy et MacNeal) (Fig. 199, *q-t*). In robins, *Turdus migratorius migratorius*; schizogony completed in probably 24 hours; gametocytes similar to those of *P. elongatum*; number of merozoites from a schizont 4 (4-8); 1-3 pigment granules.

P. nucleophilum Manwell (Fig. 200, *a-d*). In catbird, *Dumetella carolinensis*; schizogony completed in probably 24 hours; gametocytes elongate, sometimes curved around nucleus; merozoites 4-9; black pigment granules, massed in schizonts, often at one end in gametocytes.

P. polare Manwell (Fig. 200, *e-i*). In cliff swallow, *Petroche-*

liden lunifrons lunifrons; gametocytes elongate, often broader than in *P. elongatum*; merozoites 8-14 pigment granules, often oval, clumped; canaries not susceptible.

P. circumflexum Kikuth (Fig. 200, j-m). In red-winged black-bird, cowbird, and Juniper thrush; schizogonic cycle completed

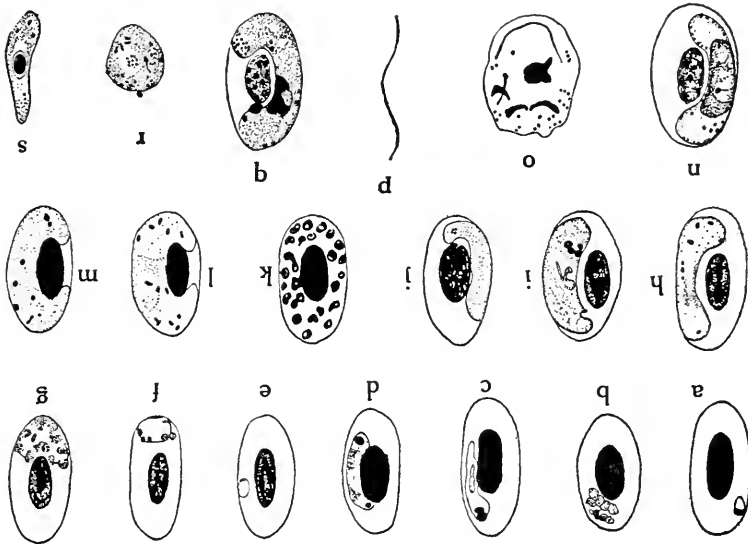


FIG. 200. a-d, *Plasmodium nucleophilum* (a, b, schizonts; c, microgametocyte; d, macrogametocyte), $\times 1330$ (Manwell); e-i, *P. polare* (e-g, schizogony; h, microgametocyte; i, macrogametocyte), $\times 1330$ (Manwell); j-m, *P. circumflexum* (j, k, schizonts; l, microgametocyte; m, macrogametocyte), $\times 1330$ (Manwell); n-s, *Haemoproteus lophortyx* (n, o, microgametocytes; p, microgamete; q, macrogametocyte; r, macrogamete; s, ookinete), $\times 1690$ (O'Roke).

in 48 hours; merozoites 13-30; small pigments scattered; gametocytes elongate, ends may curve about host cell-nucleus; sexual cycle in *Theobaldia annulata* and *T. melaneura*.

Family 2 Haemoproteidae Doflein

Schizogony occurs in endothelial cells of vertebrates; merozoites penetrate into circulating blood cells and develop into gametocytes; if blood is taken up by specific blood-sucking insects, gametocytes develop into gametes which unite to form zygotes that undergo changes similar to those stated above for the family Plasmodiidae.

Genus **Haemoproteus** Kruse. Gametocytes in erythrocytes, with pigment granules, halter-shaped when fully formed (hence *Halterium* Labbé); schizogony probably in viscera of vertebrate hosts; sexual reproduction in blood-sucking insects; in birds and reptiles.

H. columbae Celli et Sanfelice. In the pigeon, *Columba livia*; widely distributed; schizogony in endothelial cells of capillaries of lungs and other organs; sexual reproduction in, and transmission by, *Lynchia maura*, *L. brunea*, *L. lividicolor*, *L. capensis* and *Microlynchia fusilla*.

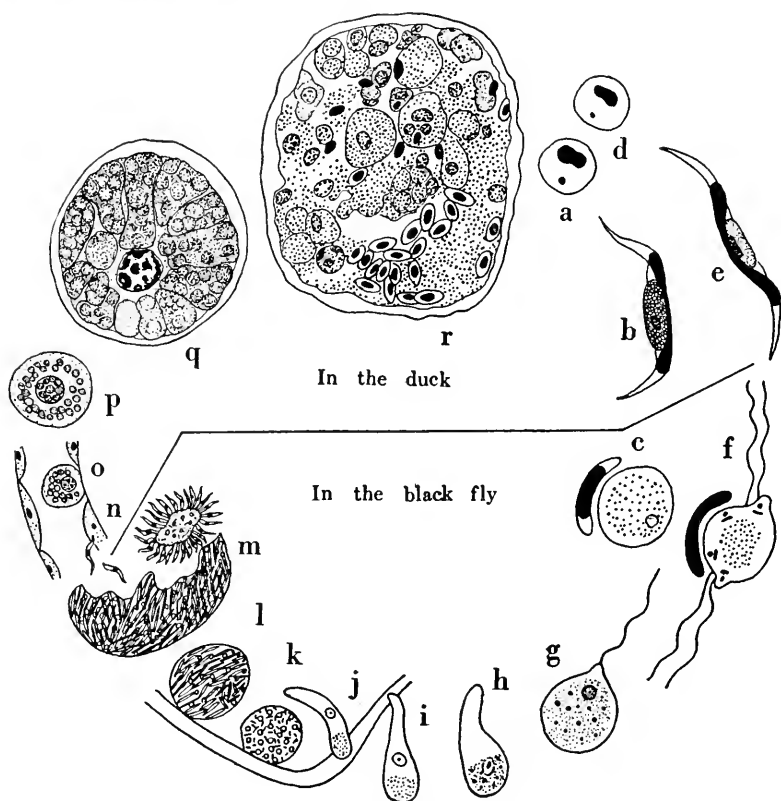


FIG. 201. The life-cycle of *Leucocytozoon anatis* (Brumpt, modified). a-c, development of macrogamete; d-f, development of microgametes; g, fertilization; h, ookinete; i, j, ookinete piercing through the stomach wall; k-m, development of sporozoites; n, sporozoites entering endothelial cells; o-r, schizogony.

H. lophortyx O'Roke (Fig. 200, *n-s*). In California Valley quail, *Lophortyx* spp.; gametocytes in erythrocytes, also occasionally in leucocytes; young gametocytes, spherical to elongate, about 1μ long; more developed forms, cylindrical, about 8μ by 2μ , with 2–10 pigment granules; mature gametocytes, halter-shaped, encircling nucleus of host erythrocyte, 18μ by 1.5 – 2.5μ ; numerous pigment granules; 4–8 microgametes, about 13.5μ long, from each microgametocyte; on slide in one instance, gamete-formation, fertilization and ookinete formation, completed in 52 minutes at room temperature; in nature sexual reproduction takes place in the fly, *Lynchia hirsuta*, which process seems to be similar to that of Plasmodium in mosquitoes (p. 435); sporozoites enter salivary glands and fill central tubules; schizonts present in lungs, liver and spleen of quail after infected flies sucked blood from the bird; merozoites found in endothelial cells of capillaries of lungs, in epithelial cells of liver and rarely in peripheral blood cells; how merozoites enter blood cells is unknown; schizonts seldom seen in circulating blood; infected birds show pigment deposits in spleen and lungs (O'Roke).

Genus **Leucocytozoon** Danilewsky. Schizogony in endothelial cells and cells of viscera of vertebrates; sexual reproduction in blood-sucking insects; gametocytes occur in spindle cells or reticulocytes.

L. anatis Wickware (Fig. 201). In wild and domestic ducks; sexual cycle in the black fly, *Simulium venustum*. O'Roke (1934) studied the life-cycle of this sporozoan: gametocytes develop into mature gametes in 1–2 minutes after blood is obtained from an infected duck; macrogametes about 8μ in diameter; 4–8 microgametes, 15.7 – 24.1μ long, from a single microgametocyte; zygotes are found in stomach contents of fly in 10–20 minutes after sucking in infected blood of bird; motile ookinetes abundant after 5 hours, measure 33.3μ by 3 – 4.6μ ; 22 hours after sucking duck blood, oocysts found on outer wall of stomach; sporozoites mature probably in 24–48 hours; 5 days after a duck has been bitten by infected black flies, schizogonic stages are noticed in endothelial cells of capillaries of lungs, liver, spleen; on about 7th day gametocytes appear in blood; liver and spleen become hypertrophied; the infection among ducklings is said to be highly fatal and appears often suddenly.

L. simondi Mathis et Léger. Macrogametocytes oval, 14 – 15μ

by 4.5–5.5 μ , often vacuolated, nucleus with a distinct endosome; microgametocyte slightly smaller; in teal duck (*Querquedula crecca*), China. Herman (1938) observed a species of *Leucocytozoon* in common black duck (*Anas rubripes tristis*), red-breasted merganser (*Mergus serrator*) and blue-winged teal (*Querquedula discors*) and hold that *L. simondi* and *L. anatis* are one and the same species and therefore the latter name is synonymous with the former.

Family 3 Babesiidae Poche

Minute non-pigmented parasites of erythrocytes of various mammals; transmission by ticks.

Genus *Babesia* Starcovici. In erythrocytes of cattle; pear-shaped, arranged in couples; sexual reproduction in female ticks in which developing ova, hence young ticks, become infected with ookinetes, producing sporozoites which enter salivary glands (Dennis).

B. bigemina (Smith et Kilbourne) (Figs. 202; 203, *a-d*). The causative organism of the haemoglobinuric fever, Texas fever or red-water fever of cattle; the very first demonstration that an arthropod plays an important rôle in the transmission of a protozoan parasite; the infected cattle contain in their erythrocytes oval or pyriform bodies with a compact nucleus and vacuolated cytoplasm; the division is peculiar in that it appears as a budding process at the beginning. We owe Dennis (1932) for our knowledge of development of the organism.

Sexual reproduction followed by sporozoite formation occurs in the tick, *Margaropus annulatus*; when infected tick takes in infected blood into gut lumen, isogametes, 5.5–6 μ long, are produced; isogamy results in motile club-shaped ookinetes, 7–12 μ long, which pass through gut wall and invade larger ova (1–2, in one case about 50, ookinetes per egg); each ookinete rounds itself up into a sporont, 7.5–12 μ in diameter, which grows in size and whose nucleus divides repeatedly; thus are produced multinucleated (4–32 nuclei) amoeboid sporokinetes, up to 15 μ long, which now migrate throughout embryonic tissue cells of tick, many of which cells develop into salivary gland cells; sporokinetes develop into sporozoites before or after hatching of host tick; sporozoites bring about an infection to cattle when they are inoculated by tick at the time of feeding. Texas fever once caused

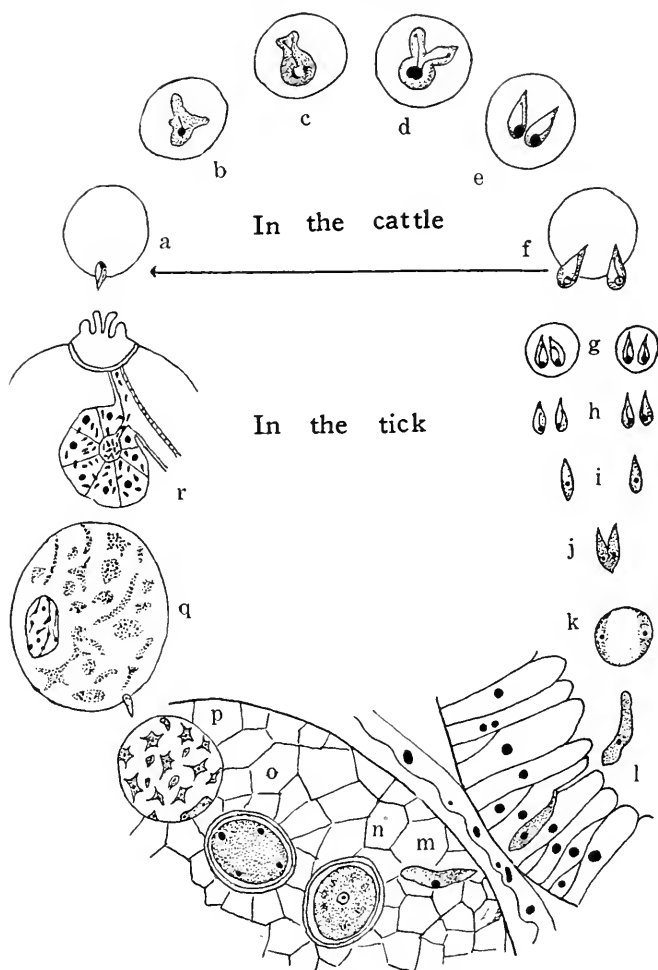


FIG. 202. The life-cycle of *Babesia bigemina* (Dennis). a-f, division in erythrocytes of cattle; g, h, gametocytes; i, isogametes; j, fertilization; k, zygote; l, ookinete penetrating through the gut wall; m, ookinete in host egg; n-p, sporoblast-formation; q, sporokinets in a large embryonic cell; r, sporozoites in salivary gland.

a considerable amount of damage to the cattle industry in the southern United States to which region the distribution of the tick is limited.

B. bovis Starcovici (Fig. 203, e-h). In European cattle; amoeboid form usually rounded, though sometimes stretched; 1-1.5 μ

in diameter; paired pyriform bodies make a larger angle, $1.5-2\mu$ long; transmitted by *Ixodes ricinus*.

Babesia occur also in sheep, goats, pigs and horses.

B. canis (Piana et Galli-Valerio). Pyriform bodies $4.5-5\mu$ long; the organism causes malignant jaundice in dogs; widely distributed; transmitted by ticks, *Haemaphysalis leachi*, *Rhipicephalus sanguineus*, and *Dermacentor reticulatus*.

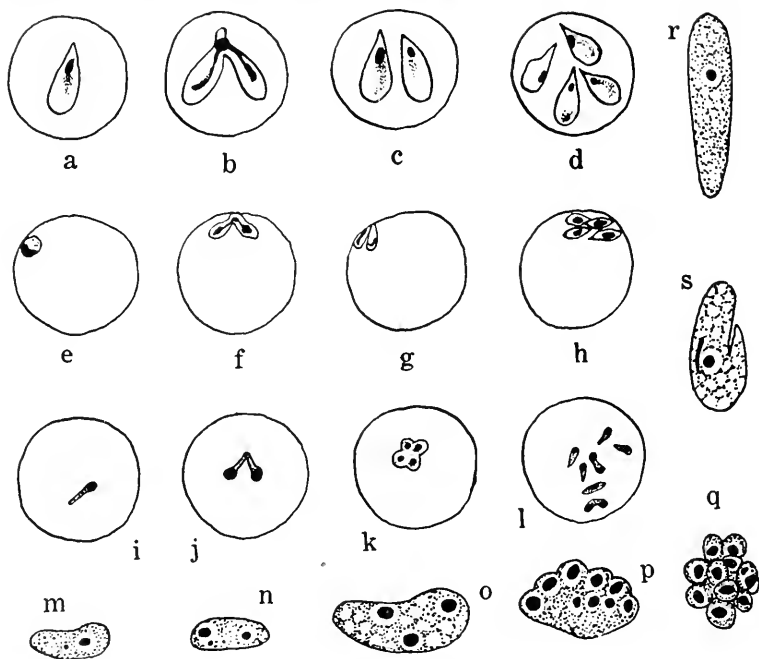


FIG. 203. a-d, *Babesia bigemina*, $\times 3000$ (Nuttall); e-h, *B. bovis*, $\times 3000$ (Nuttall); i-l, *Theileria parva*, $\times 3000$ (Nuttall); m-s, *Dactylosoma ranarum* (m-q), schizogony; r, s, gametocytes, $\times 2700$ (Nöller).

Genus **Theileria** Bettencourt, França et Borges. Schizogony takes place in endothelial cells of capillaries of viscera of mammals; certain forms thus produced enter erythrocytes and appear in peripheral circulation.

T. parva (Theiler) (Fig. 203, i-l). In cattle in Africa, cause of African coast fever; intracorpuseular forms $1-2\mu$ in diameter; transmitted by the tick, *Rhipicephalus evertsi*.

Genus **Dactylosoma** Labbé. In blood of reptiles and amphib-

ians; schizogony in erythrocytes; gametocytes also in erythrocytes; invertebrate hosts unknown.

D. ranarum (Kruse) (Fig. 203, *m-s*). In European frogs; schizonts 4–9 μ in diameter; merozoites 4–16, 2–3 μ by 1–1.5 μ ; gametocytes 5–8 μ by 1.5–3 μ .

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CHAPTER 26

Subclass 2 Acnidosporidia Cépède

THE sporozoa which are provisionally grouped here are mostly incompletely known, although some of them are widely distributed among the higher vertebrates. They possess spores which are quite simple in their structure, while their development is so far as is known wholly different from that of the Telosporidia.

Muscle parasites of higher vertebrates. Order 1 Sarcosporidia
Parasites of invertebrates and fish. . . . Order 2 Haplosporidia (p. 448)

Order 1 Sarcosporidia Balbiani

These sporozoans are characteristic muscle parasites of mammals, although reptiles and birds have also been found to harbor them. The spore which has been known as **Rainey's corpuscle**, is crescent-shaped (Fig. 205). One end is rounded and the other pointed. Near one end there is a single nucleus, and the cytoplasm contains numerous granules. Infection of a new host begins with the entrance of spores into the digestive tract of a specific animal through mouth. The delicate spore membrane ruptures and the sporozoite is liberated, which enters the gut-epithelium. After multiplying in this situation, the organism makes its way into the muscular tissue. At the beginning the parasitic mass is an elongated multinucleate body which may or may not divide into as

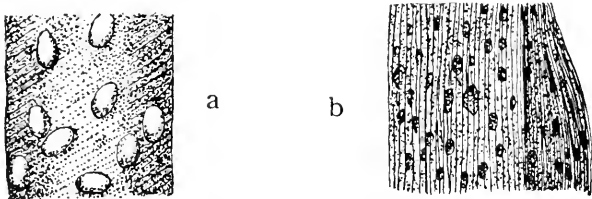


FIG. 204. a, *Sarcocystis tenella* in the oesophagus of sheep; b, *S. miescheriana* in the muscle of pig; $\times 1$ (Schneidemühl from Doflein).

many uninucleate bodies as there are nuclei. These become the centers of infection in other muscle fibers. Some trophozoites grow in size and the body becomes divided into parts, in each of which spores are formed (Fig. 205). Some authors believe that the

spores themselves are capable of fission. The host muscle fiber harboring the trophozoite, may vary in size from microscopic to as large as 5 centimeters (Fig. 204). They are cylindrical with more or less pointed extremities and with a somewhat lobulated surface, and opaque whitish. They were formerly called **Miescher's tubes** (Fig. 204).

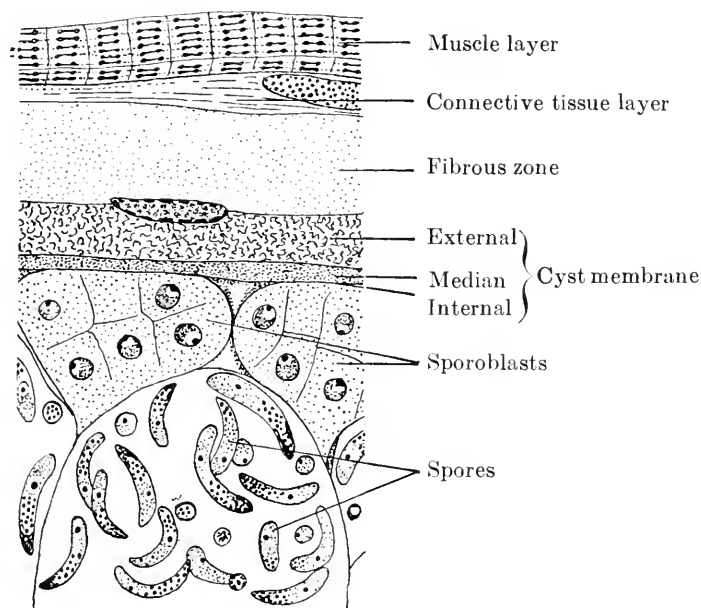


FIG. 205. Portion of a cyst of *Sarcocystis tenella* in sheep, \times about 1000 (Alexeieff).

As to the pathogenic effect of the parasites upon the host animal, fatal cases are not uncommon. In heavily infected animals extensive muscular degeneration appears and the hosts die, soon or later, from the infection. One peculiarity of the Sarcosporidia is that these organisms contain certain toxin, sarcocystine, and which when injected is highly toxic to other animals.

Genus **Sarcocystis** Lankester. In muscles of vertebrates; numerous species have been described from various mammals on the basis of difference in host species and slight difference in dimensions of spore. They are, however, morphologically indistinguishable from one another.

S. lindemanni (Rivolta). In man; rare; in muscle fibers of

larynx (Baraban and St. Remy), in muscles of biceps and tongue (Darling), in cardiac muscles (Manifold), etc.; parasites in muscles. 1.6 mm. by 170μ , elongate spindle, wall thin, contents divided into numerous chambers, spores banana-form, $8-9\mu$ long (Baraban and St. Remy); parasites 84μ by 27μ , spores 4.25μ by 1.75μ (Darling); parasites spherical, 500μ in diameter (Manifold).

S. tenella Railliet (Figs. 204, *a*; 205). In muscles of tongue, pharynx, oesophagus, larynx, neck, heart, etc., of sheep; large parasites $40\mu-2$ cm. long with a thin membrane; spores sickle-form.

S. miescheriana (Kühn) (Fig. 204, *b*). In muscles of pig; parasitic mass up to 3–4 mm. by 3 mm; envelope striated; spores reniform, capable of division when young (Manz).

S. bertrami Dofflein. In muscles of horses; similar to *S. miescheriana*; parasitic mass up to 9–10 mm; envelope striated.

S. muris Blanchard. In body muscles of rats and mice; parasitic masses up to 3 cm; spores $13-15\mu$ by $2.5-3\mu$; transmissible to guinea pig (Negri) which shows infection in muscles in 50–100 days after feeding on infected muscles.

Order 2 Haplosporidia Caullery et Mesnil

This order includes those sporozoans which produce simple spores. In some species the spores may resemble superficially those of Microsporidia, but do not possess the polar filament. The exact boundaries and affinities of this order to other groups are to be determined by future investigators.

The Haplosporidia are cytozoic, histozoic, or coelozoic parasites of invertebrates and lower vertebrates. The spore is spherical or ellipsoidal in form and covered by a resistant membrane which may possess ridges or may be prolonged into a more or less long tail-like projection. In a few species the spore membrane possesses a lid which, when opened, will enable the sporoplasm to emerge as an amoebula. The sporoplasm is uninucleate and fills the intrasporal cavity.

The development of a haplosporidian, *Ichthyosporidium giganteum*, as worked out by Swarezewsky, is as follows (Fig. 206): The spores germinate in the alimentary canal of the host fish and the sporoplasms make their way to the connective tissue of various organs (*a*). These amoebulae grow and their nuclei multiply in

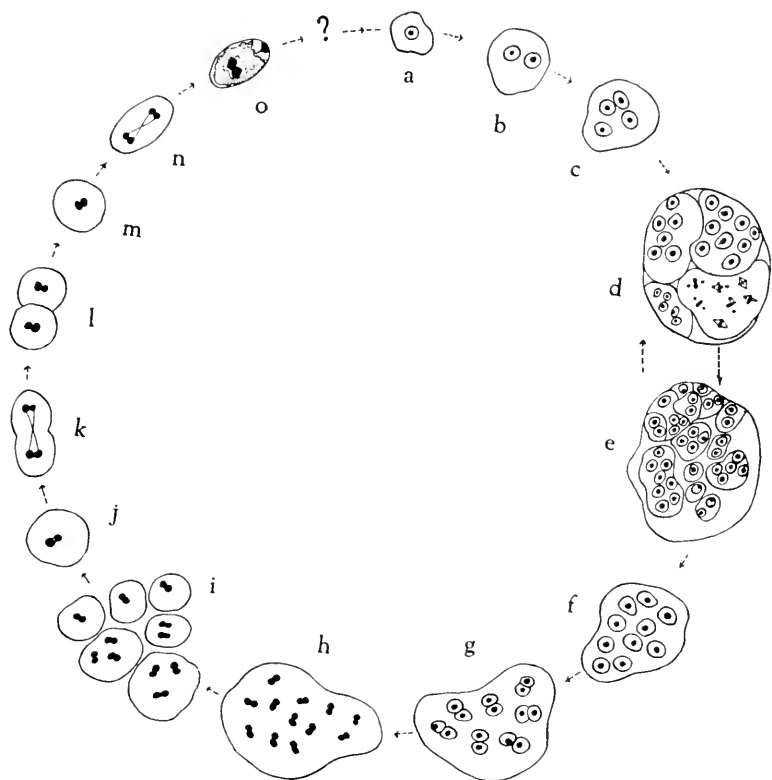


FIG. 206. The development of *Ichthyosporidium giganteum* (Swarzewsky). a-e, schizogony; f-n, sporogony; o, stained spore, \times about 1280.

number, thus forming plasmodia. The plasmodia divide into smaller bodies, while the nuclei continue to divide (*b-e*). Presently the nuclei become paired (*f, g*) and the nuclear membranes disappear (*h*). The plasmodia now break up into numerous small bodies, each of which contains one set of the paired nuclei (*i, j*). This is the sporont (*j*) which develops into 2 spores by further differentiation (*k-o*).

Genus **Haplosporidium** Caullery et Mesnil. After growing into a large form, plasmodium divides into uninucleate bodies, each of which develops into a spore; spore truncate with a lid at one end; envelope sometimes prolonged into processes; in aquatic annelids and molluscs.

H. chitonis (Lankester) (Fig. 207, a, b). In liver and connective

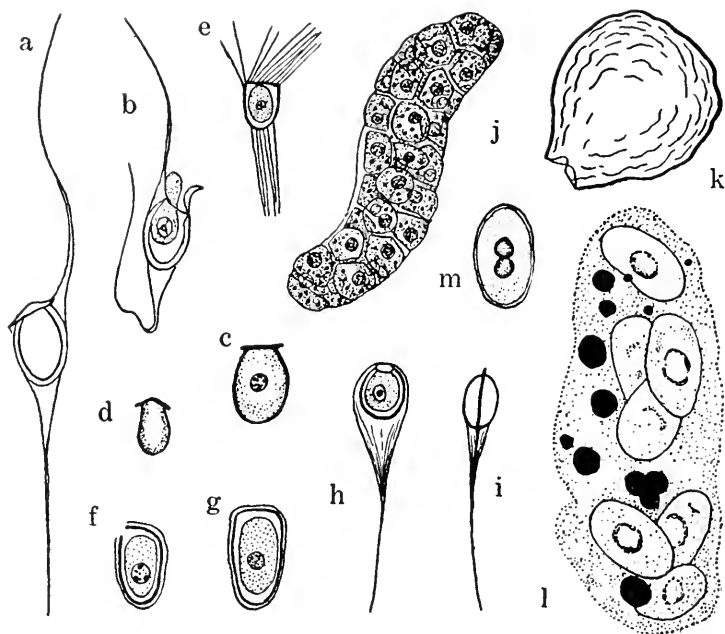


FIG. 207. a, b, *Haplosporidium chitonis*, $\times 1000$ (Pixell-Goodrich); c, *H. limnodrili*, $\times 1000$ (Granata); d, *H. nemertis*, $\times 1000$ (Debaisieux); e, *H. heterocirri*, $\times 1000$ (Caullery and Mesnil); f, *H. scolopli*, $\times 1000$ (Caullery and Mesnil); g, *H. vej dovskii*, $\times 1000$ (Caullery and Mesnil); h, i, *Urosporidium fuliginosum*, $\times 1000$ (Caullery and Mesnil); j, k, *Bertramia asperospora* (j, cyst with spores; k, empty cyst), $\times 1040$ (Minchin); l, m, *Coelosporidium periplanetae* (l, trophozoite with spores and chromatoid bodies), $\times 2540$ (Sprague).

tissue of *Craspidochilus cinereus*; spores oval, 10μ by 6μ ; envelope with 2 prolonged projections.

H. limnodrili Granata (Fig. 207, c). In gut epithelium of *Limnodrilus udekemianus*; spores $10\text{--}12\mu$ by $8\text{--}10\mu$.

H. nemertis Debaisieux (Fig. 207, d). In connective tissue of *Lineus bilineatus*; spores oval with a flat operculum, but without any projections of envelope, 7μ by 4μ .

H. heterocirri C. et M. (Fig. 207, e). In gut epithelium of *Heterocirrus viridis*; mature organisms $50\text{--}60\mu$ by $30\text{--}40\mu$; spores 6.5μ by 4μ .

H. scolopli C. et M. (Fig. 207, f). In *Scoloplos mulleri*; fully grown form $100\text{--}150\mu$ by $20\text{--}30\mu$; spores 10μ by 6.5μ .

H. vejvodskii C. et M. (Fig. 207, *g*). In a freshwater oligochaete, *Mesenchytraeus flavus*; spores 10–12 μ long.

Genus **Urosporidium** Caullery et Mesnil. Similar to *Haplosporidium*, but spherical spore with a long projection.

U. fuliginosum C. et M. (Fig. 207, *h, i*). In coelom of the polychaete, *Syllis gracilis*; rare.

Genus **Anurosporidium** Caullery et Chappellier. Similar to *Haplosporidium*, but operculate spore spherical.

A. pelseeneeri C. et C. In sporocyst of a trematode parasitic in *Donax trunculus*; schizogony intracellular; cysts extracellular, with up to 200 spores; spores about 5 μ long.

Genus **Bertramia** Caullery et Mesnil. Parasitic in aquatic worms and rotifers; sausage-shaped bodies in coelom of host; spherical spores which develop in them, possess a uninucleate sporoplasm and a well-developed membrane.

B. asperospora (Fritsch) (Fig. 207, *j, k*). In body cavity of rotifers: Brachionus, Asplanchna, Synchaeta, Hydatina, etc.; fully grown vermicular body 70–90 μ with 80–150 spores.

B. capitellae C. et M. In the annelid *Capitella capitata*; spores 2.5 μ in diameter.

B. euchlanis Konsuloff. In coelom of rotifers belonging to the genus Euchlanis.

Genus **Ichthyosporidium** Caullery et Mesnil. In fish; often looked upon as Microsporidia, as the organism develops into large bodies in body muscles, connective tissue, or gills, which appear as conspicuous "cysts," which are surrounded by a thick wall and contain numerous spores.

I. giganteum (Thélohan) (Fig. 206). In various organs of *Crenilabrus melops* and *C. ocellatus*; cysts 30 μ –2mm. in diameter; spores 5–8 μ long.

I. hertwigi Swarezewsky. In *Crenilabrus paro*; cysts 3–4 mm. in diameter in gills; spores 6 μ long.

Genus **Coelosporidium** Mesnil et Marchoux. In coelom of Cladocera or Malpighian tubules of cockroach; body small, forming cysts; spores resemble microsporidian spores; but without a polar filament.

C. periplanetae (Lutz et Splendore) (*C. blattellae* Crawley) (Fig. 207, *l, m*). In lumen of Malpighian tubules of cockroaches; common; spores 5.5–7.5 μ by 3–4 μ . Some authors consider this a microsporidian.

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CHAPTER 27

Subclass 3 **Cnidosporidia** Doflein

THE members of this subclass possess without exception resistant **spores** which are of unique structure. Each spore possesses 1–4 **polar capsules** and one to many **sporoplasms**. The membrane which envelops these structures may be a single-piece or bi- or tri-valved. Within each of the polar capsules is coiled a **polar filament**.

In the order Myxosporidia and Actinomyxidia, there appear several cells during the process of sporulation. These cells give rise to one to many sporoplasms, or generative cells, capsulogenous cells, and spore membrane. This condition is not observed in other groups of Protozoa and for this reason some writers recognize a close affinity between these two orders and the Mesozoa. The method of multiplication in the Cnidosporidia is schizogonic and sporogonic. The schizogony is binary or multiple fission, budding, or plasmotomy. The nuclear division varies from amitosis to mitosis. Isogamous, anisogamous, and autogamous reproduction have been reported in a number of forms. In many forms, the zygote is the sporont, in which one to many spores become differentiated.

No secondary or intermediate host has been found for any of the Cnidosporidia. They are exclusively parasites of the lower vertebrates and invertebrates. Since cnidosporidian infections occur frequently in epidemic forms among such economically important animals as the silkworm, honey bees, and commercial fishes, the organisms possess considerable practical significance.

Spores comparatively large

Shell bivalve; 1, 2, or 4 polar capsules. Order 1 Myxosporidia (p. 454)

Shell trivalve; 3 polar capsules. Order 2 Actinomyxidia (p. 468)

Spores comparatively small

Shell one-piece; 1 (or 2) polar filament. Order 3 Microsporidia (p. 472)

Barrel-shaped; a thick filament coiled beneath the shell; 3 sporoplasms Order 4 Helicosporidia (p. 479)

Order 1 **Myxosporidia** Bütschli

The spore of a myxosporidian is of various shapes and dimensions. It is covered by a bivalve chitinous **spore membrane**, the two valves meeting in a **sutural plane** which is either twisted (in three genera) or more or less straight. The membrane may possess various markings or processes. The **polar capsule**, with its short coiled **filament**, varies in number from one to four. Except in the family Myxidiidae, in which one polar capsule is situated near each of the poles of the spore, the polar capsules are always grouped at one end which is ordinarily designated as the anterior end of the spore. Below or between (in Myxidiidae) the polar capsules, there is almost always a **sporoplasm**. Ordinarily a young spore possesses two nuclei which fuse into one (autogamy) when the spore becomes mature. In Myxobolidae there is a glycogenous substance in a vacuole which stains mahogany red with iodine and which is known as the **iodinophilous** (iodophile) **vacuole**.

The Myxosporidia are almost exclusively parasites of lower vertebrates, especially fishes. Both fresh and salt water fishes have been found to harbor, or to be infected by, Myxosporidia in various regions of the world. A few occur in Amphibia and Reptilia, but no species has been found to occur in either birds or mammals. When a spore gains entrance into the digestive tract of a specific host fish, the **sporoplasm** leaves the spore as an **amoebula** which penetrates through the gut-epithelium and, after a period of multiplication, enters the tissues of certain organs, where it grows into a **schizont** at the expense of the host tissue cells, and the nucleus divides repeatedly. Some nuclei become surrounded by masses of cytoplasm and become the **sporonts** (Fig. 208). The sporonts grow and their nuclei divide several times, forming 6–18 daughter nuclei, each with a small mass of cytoplasm. The number of the nuclei thus produced depends upon the structure of the mature spore, and also upon whether 1 or 2 spores develop in a sporont. When the sporont develops into a single spore, it is called a monosporoblastic sporont, and if two spores are formed within a sporont, which is usually the case, the sporont is called disporoblastic, or **pansporoblast**. The spore-formation begins usually in the central area of the large trophozoite, which continues to grow. The surrounding host tissue becomes degenerated or modified and forms an envelope which is often large enough to be visible to the naked eye. This is ordi-

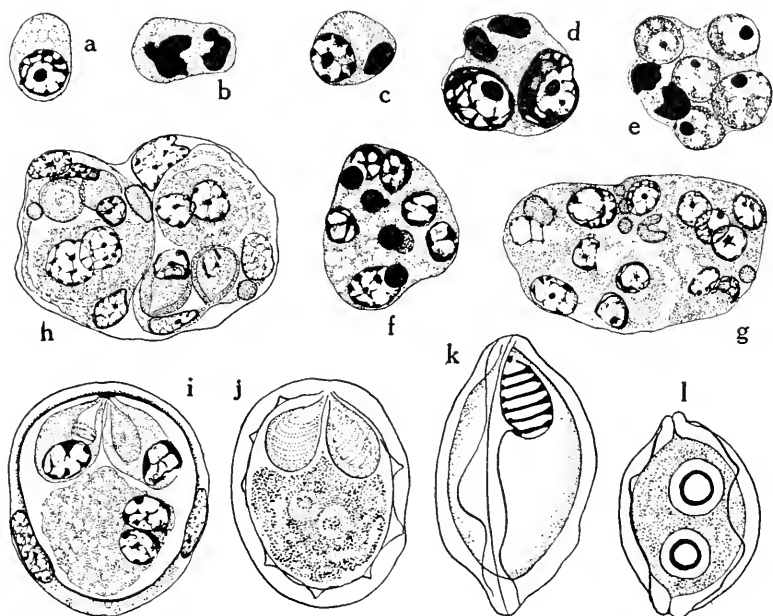


FIG. 208. Sporogony in *Myxosoma catostomi*, $\times 2130$ (Kudo). a, sporont or pansporoblast; b-h, development of two sporoblasts within the sporont; i, a nearly mature spore; j-l, views of spore.

narly referred to as a **myxosporidian cyst**. If the site of infection is near the body surface, the large cyst breaks and the mature spores become set free in the water. In case the infection is confined to internal organs, the spores will not be set free while the host fish lives. Upon its death and disintegration of the body, however, the liberated spores become the source of new infection.

The more primitive Myxosporidia are coelozoic in the host's organs, such as the gall bladder, uriniferous tubules of the kidney, urinary bladder, etc. In these forms, the liberated amoebulae make their way into the specific organ and there grow into multinucleate amoeboid trophozoites which are capable of forming pseudopodia of various types. They multiply by exogenous or endogenous budding or plasmotomy. One to several spores are developed in the trophozoite.

Almost all observers agree in maintaining the view that the 2 nuclei of the sporoplasm or 2 uninucleate sporoplasms fuse into one (autogamy or paedogamy), but as to the nuclear as well as

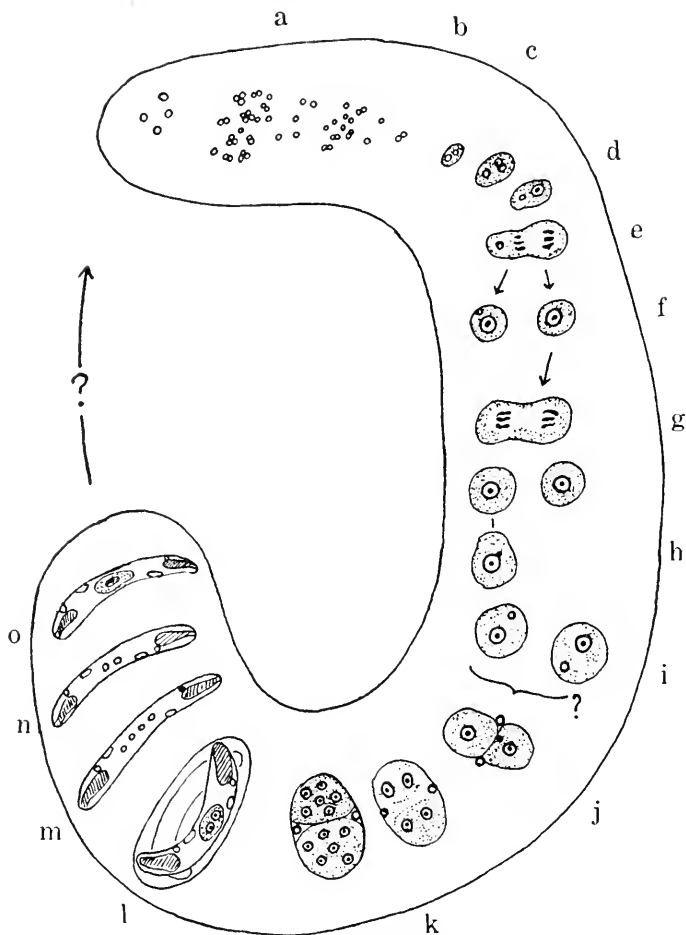


FIG. 209. The development of *Sphaeromyxa sabrazesi* (Debaisieux). a, vegetative nuclei; b, association of two vegetative nuclei; c, the same within a cell; d, primary propagative cell; e, its division; f, secondary propagative cells; g, their division; h, formation of sporocyte; i, two sporocytes; j, formation of pansporoblast; k, pansporoblast at later stage; l, pansporoblast with two spores, the sporoplasm of which contains two nuclei; m, four nuclei in sporoplasm; n, two nuclei remain functional, the other two degenerate; o, fusion of the two nuclei.

cytoplasmic changes prior to, and during, spore-formation, there is a diversity of opinions. To illustrate the views held by those who believe there is a sexual phase in the development of a myxosporidian, *Sphaeromyxa sabrazesi* (p. 465) may be taken as an

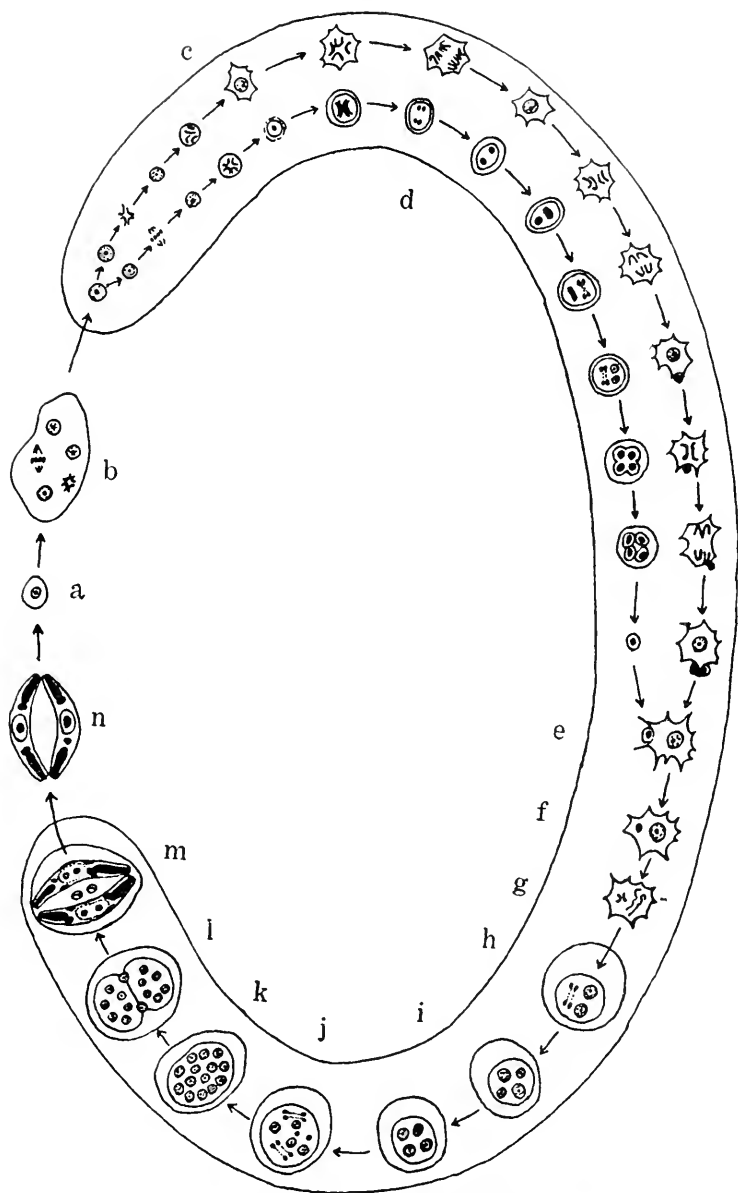


FIG. 210. The development of *Sphaeromyxa sabrazesi* (Naville). a, uninucleate amoebula enters the gall bladder; b, young multinucleate trophozoite; c, development of macrogametes; d, development of microgametes; e, f, plasmogamy; g-m, development of pansporoblast; n, fusion of the two nuclei in the sporoplasm.

example. Debaisieux's observation on this myxosporidian is in brief as follows (Fig. 209): sporoplasms after finding their way into gall bladder of host fish develop into large trophozoites containing many nuclei (*a*), 2 vegetative nuclei become surrounded by a cytoplasmic mass (*c*) and this develops into a primary propagative cell (*d*) which divides (3 chromosomes are noted) (*e*) and forms secondary propagative cells (*f*). A binucleate **sporocyte** is formed from the latter by unequal nuclear division (*g-i*) and 2 sporocytes unite to form a tetranucleate pansporoblast (*j*) which develops into 2 spores (*k, l*). Sporoplasm first shows 2 nuclei, but later 4, of which 2 degenerate and the other 2 fuse into one nucleus. On the other hand, according to Naville (1930) uninucleate amoebula (Fig. 210, *a*) enters the gall bladder and develops into multinucleate trophozoite in which nuclear division reveals 4 chromosomes (*b*); within the trophozoite macrogametes and microgametes are independently formed, during which process, chromosome number is reduced into half (2) (*c, d*); plasogamy between a macrogamete and a microgamete results in production of a binucleate pansporoblast (*e, f*), from which repeated nuclear division (*g-l*) forms 2 spores (*m*); each of the 2 nuclei of the sporoplasm is haploid and the diploid number is restored when the 2 nuclei fuse into one (*n*).

The site of infections by Myxosporidia varies among different species. They have been found in almost all kinds of tissues and organs of host fish, although each myxosporidian has its special site of infection in one to several species of fish. The gills and gall bladder are most frequently parasitized by Myxosporidia in

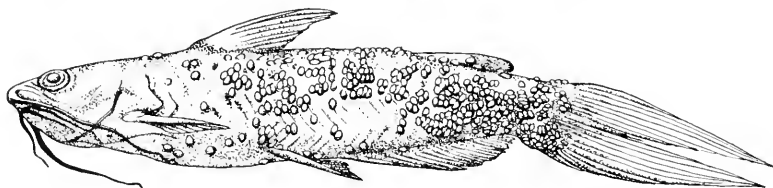


FIG. 211. A channel cat, heavily infected with *Henneguya crilis*, $\times \frac{1}{2}$ (Kudo).

freshwater fishes, while the gall bladder and urinary bladder of marine fishes harbor one or more species of Myxosporidia. When the infection is concentrated in the fins or integument, the resulting changes are quite conspicuous (Fig. 211). The infection in

the gills is usually manifest by whitish pustules which can be frequently detected with the unaided eye. When the wall of the alimentary canal, mesentery, liver, and other organs are attacked, one sees considerable changes in them. Heavy myxosporidian infection of the gall bladder or urinary bladder of the host fish may cause abnormal appearance and coloration or unusual enlargement of the organ, but under ordinary circumstances the infection is detected only by a microscopical examination of its contents. Certain histological changes in the host fish have been mentioned elsewhere (p. 26).

Severe epidemic diseases of fishes are frequently found to be due to myxosporidian infections. According to Davis, the "wormy" halibut of the Pacific coast of North America is due to the myxosporidian, *Uncapsula muscularis* (Fig. 213), which invades the muscular tissue of the host fish. The "boil disease" of the barbel, *Barbus barbus* and others, of European waters, is caused by *Myxobolus pfeifferi*. *Myxosoma cerebralis* which attacks the supporting tissues of salmonoid fish, is known to be responsible for the so-called "twist disease," which is often fatal, especially to young fishes and which occurs in an epidemic form.

The Myxosporidia are divided into three suborders:

- Largest diameter of spore at right angles to sutural plane; with 1 polar capsule on each side; sporoplasm without iodophilous vacuole
.....Suborder 1 Eurysporea
- Spore spherical or subspherical with 1, 2, or 4 polar capsules; sporoplasm without iodophilous vacuole. . . .
.....Suborder 2 Sphaerosporea (p. 461)
- Sutural plane coincides with, or is at an acute angle to, largest diameter of spore; 1, 2, or 4 polar capsules; sporoplasm with or without iodophilous vacuole.Suborder 3 Platysporea (p. 464)

Suborder 1 **Eurysporea** Kudo

- Spores laterally expanded; coelozoic in marine fish, except one species
.....Family 1 Ceratomyxidae
- Spores less laterally expanded; in freshwater fish; holozoic or coelozoic
.....Family 2 Wardiidae (p. 461)

Family 1 **Ceratomyxidae** Doflein

Spores are laterally prolonged and therefore sutural diameter is smaller than width; 2 polar capsules at anterior margin; one on each side of sutural plane.

Genus **Ceratomyxa** Thélohan. Shell-valves conical and hollow,

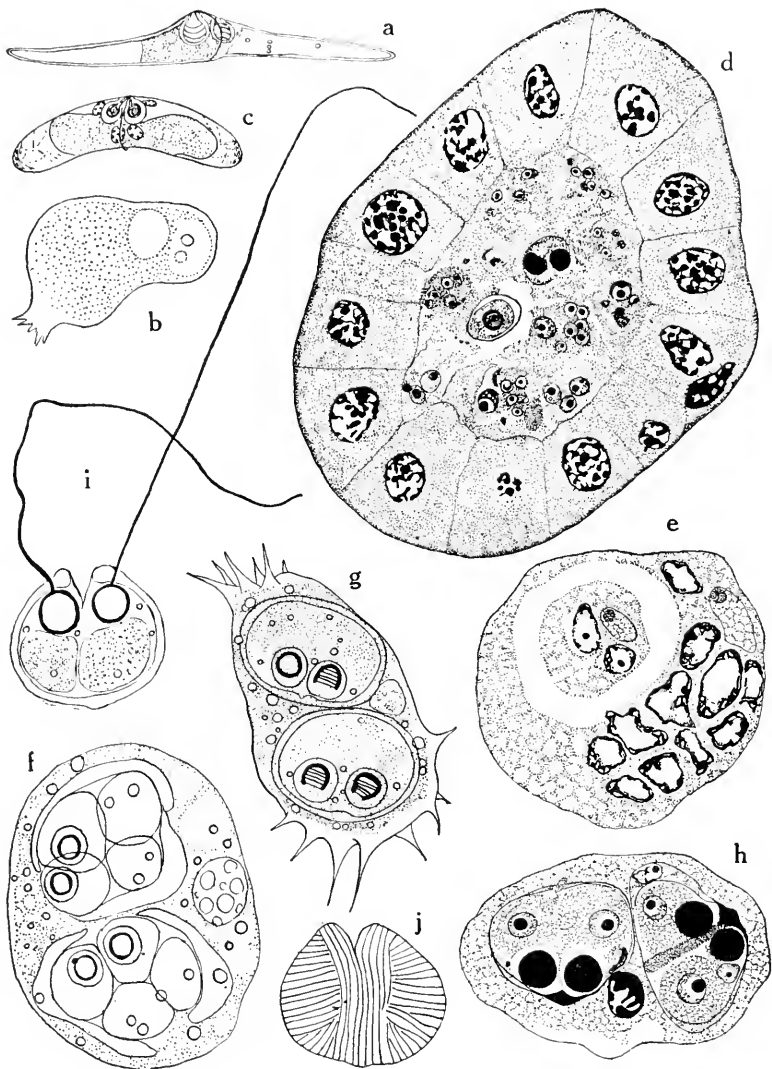


FIG. 212. a, *Ceratomyxa mesospora*, $\times 1000$ (Davis); b, c, *C. hopkinsi*, $\times 1000$ (Jameson); d-j, *Leptotheca ohlmacheri* (d, section of a uriniferous tubule of *Rana pipiens*, with trophozoites and spores, $\times 800$; e, a trophozoite with a bud; f-h, disporous trophozoites; i, a spore with extruded polar filaments; j, surface view of spore, $\times 1500$) (Kudo).

attached on bases; sporoplasm usually not filling intrasporal cavity; in gall-bladder of marine fish. Numerous species.

C. mesospora Davis (Fig. 212, *a*). In gall-bladder of *Cestracion zygaena*; spores, 8μ in sutural diameter and $50-65\mu$ wide.

C. hopkinsi Jameson (Fig. 212, *b, c*). In gall-bladder of *Parophrys vetulus*, *Microstomus pacificus* and *Citharichthys xanthostigmus*; trophozoites disporous; spores $5.7-7.5\mu$ in sutural diameter and $28.8-39\mu$ broad.

Genus **Leptotheca** Thélohan. Shell-valves hemispherical; in gall-bladder or urinary bladder of marine fish and one in amphibians. Numerous species.

L. ohlmacheri (Gurley) (Fig. 212, *d-j*). In uriniferous tubules of kidney of frogs and toads; spores $9.5-12\mu$ in sutural diameter and $13-14.5\mu$ wide.

Genus **Myxoproteus** Doflein. Spores pyramidal with or without distinct processes at base of pyramid; in urinary bladder of marine fish. 3 species.

M. cordiformis Davis (Fig. 214, *a*). In urinary bladder of *Chaetodipterus faber*; spores 12μ by $10-11\mu$.

Family 2 Wardiidae Kudo

Genus **Wardia** Kudo. Spores isosceles triangle with 2 convex sides; oval in profile; 2 large polar capsules; tissue parasites of freshwater fish. 2 species.

W. ovinocua K. (Fig. 214, *b*). In ovary of *Lepomis humilis*; spores $9-11\mu$ in sutural diameter and $10-12\mu$ wide.

Genus **Mitraspora** Fujita. Spores circular or ovoidal in front view; somewhat flattened in profile; 2 polar capsules; shell striated; with or without posterior filaments; in kidneys of freshwater fishes. This genus apparently includes border-line forms between this and other suborders. 3 species.

M. elongata Kudo. In kidney of *Apomotis cyanellus*; spores $15-17\mu$ by $5-6\mu$.

Suborder 2 Sphaerosporaea Kudo

Spore with 1 polar capsule.....Family 1 Unicapsulidae
 Spore with 2 polar capsules.....Family 2 Sphaerosporidae (p. 462)
 Spore with 4 polar capsules.....Family 3 Chloromyxidae (p. 464)

Family 1 Unicapsulidae Kudo

Genus **Unicapsula** Davis. Spherical spore with 1 polar capsule;

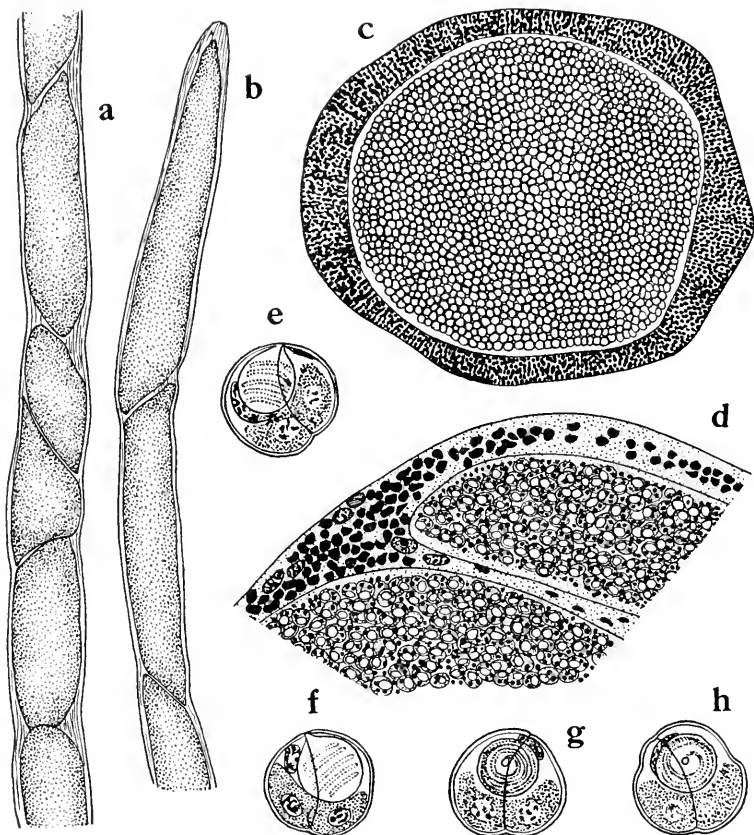


FIG. 213. *Unicapsula muscularis* (Davis). a, b, infected muscle fibers, $\times 20$; c, cross-section of an infected muscle, $\times 190$; d, $\times 575$; e-h, spores, $\times 2500$.

shell-valves asymmetrical; sutural line sinuous; histozoic in marine fish. One species.

U. muscularis D. (Fig. 213). Spore about 6μ in diameter; 2 uninucleate sporoplasms; in muscle fibers of halibut, Pacific coast of North America; the cause of the "wormy" halibut (Davis).

Family 2 Sphaerosporidae Davis

Genus **Sphaerospora** Thélohan. Spore spherical or subspherical; sutural line straight; 2 polar capsules at anterior end; coelozoic or histozoic in marine or freshwater fishes.

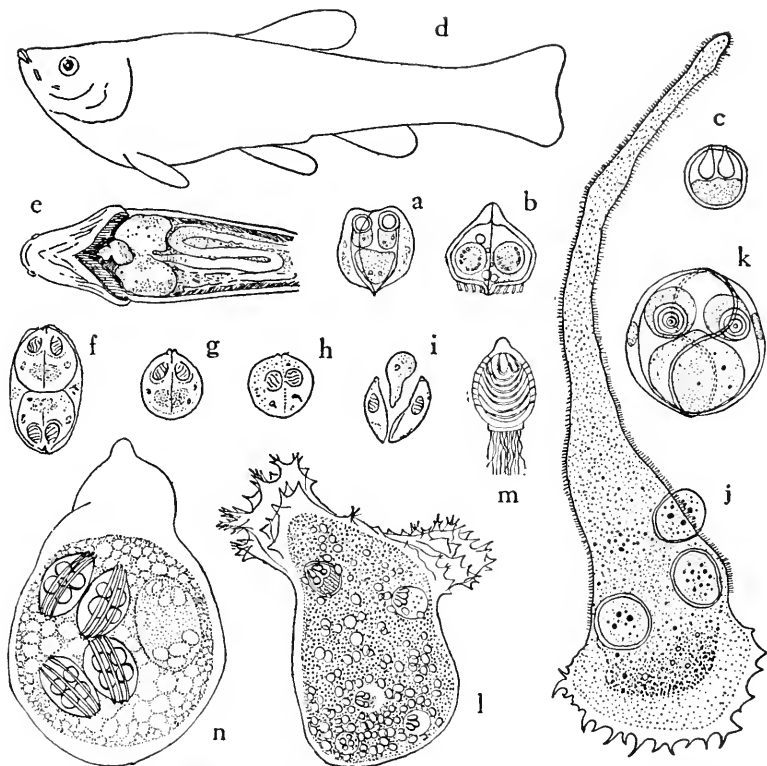


FIG. 214. a, *Myxoproteus cordiformis*, $\times 1000$ (Davis); b, *Wardia ovinocua*, $\times 1330$ (Kudo); c, *Sphaerospora polymorpha*, $\times 1000$ (Davis); d-i, *S. tincae* (d, external appearance of a heavily infected young tench; e, internal appearance, $\times \frac{1}{3}$; f, mature pansporoblast; g, h, two spores; i, germination of spore, $\times 1000$) (Léger); j, k, *Sinuolinea dimorpha* (j, trophozoite with three gemmules, $\times 420$; k, $\times 930$) (Davis); l, m, *Chloromyxum leydigi* (l, $\times 500$; m, $\times 1000$) (Thélohan); n, *C. trijugum*, $\times 1130$ (Kudo).

S. polymorpha Davis (Fig. 214, c). In urinary bladder of *Opsaus tau*; spores 7-10 μ in diameter.

S. tincae Plehn (Fig. 214, d-i). In pronephros and other viscera of *Tinca tinca* in France and Germany; cause of epidemic disease among young tench; disease is manifest by great distension of anterior portion of abdomen and up-turned mouth; infection fatal through rupture of abdominal wall; spores 7-8.75 μ in diameter.

Genus **Sinuolinea** Davis. Spherical or subspherical spores; sutural line sinuous; with or without lateral processes; 2 spherical polar capsules; in urinary bladder of marine fish.

S. dimorpha D. (Fig. 214, *j, k*). In *Cynoscion regalis*; spores 15μ in diameter.

Family 3 **Chloromyxidae** Thélohan

Genus **Chloromyxum** Mingazzini. Spore with 4 polar capsules, grouped at anterior end; shell surface often striated or ridged; sutural line frequently obscure; histozoic or coelozoic in fresh-water or marine fish and also in amphibians. Numerous species.

C. leydigi M. (Figs. 65, *e, d*; 214, *l, m*). In gall-bladder of various species of *Raja*, *Torpedo* and *Cestracion*; spores $6-9\mu$ by $5-6\mu$; widely distributed.

C. trijugum Kudo (Fig. 214, *n*). In gall-bladder of *Xenotis megalotis* and *Pomoxis sparoides*; spores $8-10\mu$ by $5-7\mu$.

Suborder 3 **Platysporea** Kudo

Without indinophilous vacuole

2 polar capsules, one at each pole. Family 1 Myxidiidae

1 polar capsule. Family 2 Coccomyxidae (p. 466)

2 or 4 polar capsules grouped. Family 3 Myxosomatidae (p. 466)

With an iodophilous vacuole. Family 4 Myxobolidae (p. 466)

Family 1 **Myxidiidae** Thélohan

Genus **Myxidium** Bütschli. Spores fusiform with pointed or rounded ends; polar filament comparatively long, fine; coelozoic or histozoic in fishes, also in amphibians and reptiles. Numerous species.

M. lieberkuhni Bütschli (Figs. 65, *a, b*; 215, *a-d*). In urinary bladder of *Esox* spp.; spores $18-20\mu$ by $5-6\mu$; widely distributed.

M. immersum (Lutz) (Fig. 215, *e, f*). In gall-bladder of various species of toads and frogs, including *Bufo* sp., and *Rana pipiens*, U.S.A.; trophozoites large rounded disc, thin, up to 3 mm. in diameter; disporoblastic; polysporous; spores with $7-9$ conspicuous transverse ridges, about 12μ by 7μ .

M. kudo Meglitsch. In gall-bladder of *Ictalurus fureatus*; trophozoites large disc-like, up to 1 mm. in diameter; spores $8.5-12\mu$ long by $4-6\mu$.

Genus **Sphaeromyxa** Thélohan. Spore fusiform, but ends usually truncate; polar filament short, thick; trophozoites large, discoid; coelozoic in marine fish. Several species.

S. balbianii T. (Figs. 65, e; 215, g-i). In gall-bladder of *Motella* and other marine fish in Europe and of *Siphostoma* in the United States; spores 15-20 μ by 5-6 μ .

S. sabraesi Laveran et Mesnil (Figs. 209, 210; 215, j-l). In gall-bladder of *Hippocampus*, *Motella*, etc.; spores 22-28 μ by 3-4 μ .

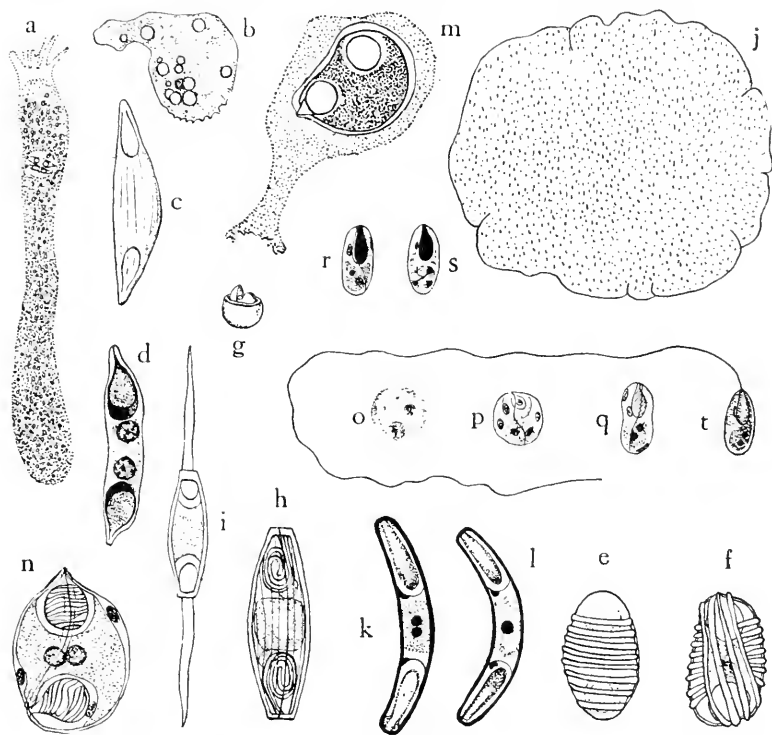


FIG. 215. a-d, *Myxidium lieberkuhni* (a, a trophozoite, $\times 220$ (Lieberkühn); b, a small trophozoite, $\times 1000$; c, d, spores, $\times 1400$) (Kudo); e, f, *M. immersum*, $\times 1400$ (Kudo); g-i, *Sphaeromyxa balbianii* (g, $\times \frac{2}{3}$; h, a spore, $\times 1400$ (Davis); i, spore with extruded polar filaments, $\times 840$ (Thélohan)); j-l, *S. sabraesi* (j, $\times 10$; k, l, spores, $\times 1000$) (Schröder); m, n, *Zschokkella hildae* (m, $\times 600$; n, $\times 1060$) (Auerbach); o-t, *Coccomyxa morovi* (o, a young binucleate trophozoite; p-s, development of sporoblast; t, a spore with the extruded polar filament), $\times 665$ (Léger and Hesse).

Genus **Zschokkella** Auerbach. Spore hemi-circular in front view; fusiform in profile; circular in cross-section; ends pointed obliquely; polar capsules large, spherical; sutural line usually in S-form, coelozoic in fish or amphibians. A few species.

Z. hildae A. (Fig. 215, *m, n*). In urinary bladder of *Gadus* spp.; spores 16–29 μ by 13–18 μ .

Family 2 **Coccomyxiidae** Léger et Hesse

Spore ellipsoidal; one polar capsule at one end; circular in cross-section; undoubtedly a border-line form between Myxosporidia and Microsporidia.

Genus **Coccomyxa** Léger et Hesse. Polar filament long, fine; coelozoic parasite in marine fish.

C. morovi L. et H. (Fig. 215, *o-t*). In gall-bladder of *Clupea pilchardus*; spores 14 μ by 5–6 μ .

Family 3 **Myxosomatidae** Poche

2 or 4 polar capsules at anterior end; sporoplasm without any iodophilous vacuoles.

Genus **Myxosoma** Thélohan (*Lentospora* Plehn). Spore circular, oval or ellipsoid in front view, lenticular in profile; 2 polar capsules at anterior end; histozoic in marine or freshwater fish. Several species.

M. catostomi Kudo (Figs. 54; 208). In muscle and connective tissue of *Catostomus commersonii*; spores 13–15 μ by 10–11.5 μ .

M. cerebralis (Hofer) (Fig. 216, *a*). In cartilage and perichondrium of salmonoid fish; young fish are especially affected by infection, the disease being known as the “twist-disease” (Drehkrankheit); spores 6–10 μ in diameter.

Genus **Agarella** Dunkerly. Spore elongate oval; 4 polar capsules at anterior end; shell prolonged posteriorly into long processes. One species.

A. gracilis D. (Fig. 216, *b*). In testis of South American lung-fish, *Lepidosiren paradoxa*.

Family 4 **Myxobolidae** Thélohan

1, 2, or 4 polar capsules grouped at anterior end; sporoplasm with iodophilous vacuole.

Genus **Myxobolus** Bütschli. Spores ovoidal or ellipsoidal, flattened; 2 polar capsules at anterior end; sporoplasm with an iodophilous vacuole; sometimes with a posterior prolongation of shell; exclusively histozoic in freshwater fish or amphibians. Numerous species.

M. Pfeifferi Thélohan (Fig. 216, *e, f*). In muscle and connective

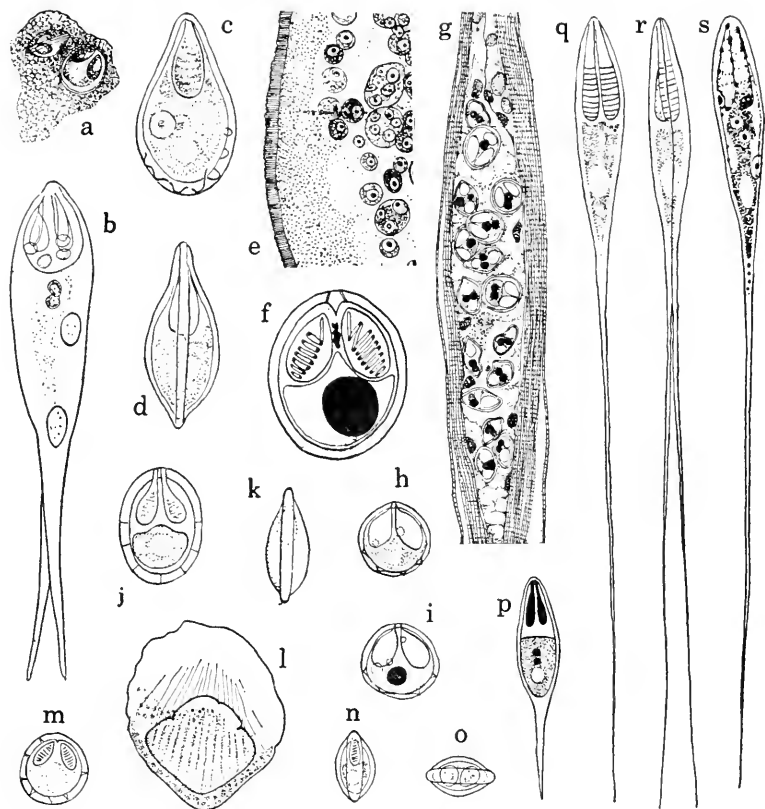


FIG. 216. a, *Myxosoma cerebralis*, $\times 800$ (Plehn); b, *Agarella gracilis*, $\times 1660$ (Dunkerley); c, d, *Thelchanellus notatus*, $\times 1530$ (Kudo); e, f, *Myxobolus pfeifferi* (e, section of a cyst; f, spore treated with Lugol, $\times 1780$) (Keysselitz); g-i, *M. orbiculatus* (g, infected muscle, $\times 600$; h, a fresh spore; i, Lugol-treated spore, $\times 1000$) (Kudo); j, k, *M. conspicuus*, $\times 1530$ (Kudo); l-o, *M. squamosus* (l, a cyst under a scale, $\times 6.5$) (Kudo); p, *Henneguya psorospermica*, $\times 1330$ (Thélohan); q-s, *H. crilis*, $\times 1530$ (Kudo).

tissue of body and various organs of *Barbus barbus*, *B. fluviatilis*, and *B. plebejus*; tumor up to a diameter of 7 cm; most of infected fish die from the effect (Keysselitz); spores $12-12.5\mu$ by $10-10.5\mu$.

M. orbiculatus Kudo (Fig. 216, g-i). In muscle of *Notropis gilberti*; spores $9-10\mu$ in diameter by $6.5-7\mu$ thick.

M. conspicuus K. (Fig. 216, j, k). In corium of head of *Moxostoma breviceps*; tumors $1/2-4$ mm.; spores $9-11.5\mu$ by $6.5-8\mu$.

M. intestinalis K. (Fig. 1, *a*). In the intestinal wall of *Pomoxis sparoides*; (fixed unstained) spores, 12–13 μ by 10–12.5 μ ; the histological changes brought about by this protozoan have been mentioned elsewhere (p. 26).

M. squamosus Kudo (Fig. 216, *l-o*). In connective tissue below scales of *Hybopsis kentuckiensis*; spore circular in front view, 8–9 μ in diameter, 4.5–5 μ thick.

Genus **Thelohanellus** Kudo. Pyriform, flattened spores, each with one polar capsule; sporoplasm with an iodophilous vacuole; histozoic in freshwater fish. 11 species.

T. notatus (Mavor) (Figs. 1, *b*; 216, *c, d*). In subdermal connective tissue of *Pimephales notatus*, *Cliola vigilax*, *Notropis cornutus*, *N. blennioides*, and *Leuciscus rutilus*; tumor up to 7 mm. in diameter; spores 17–18 μ by 7.5–10 μ ; host tissue surrounding the organism becomes so greatly changed that it appears as an epithelium (p. 26).

Genus **Henneguya** Thélohan. Spore circular or ovoidal in front view; flattened; 2 polar capsules at anterior end; each shell-valve prolonged posteriorly into a long process; sporoplasm with an iodophilous vacuole: mostly histozoic in freshwater fish. Numerous species.

H. psorospermica T. (Fig. 216, *p*). In gills of *Esox* and *Perca*; cyst formation; total length of spores 35–40 μ .

H. exilis Kudo (Figs. 211; 216, *q-s*). In gills and integument of *Ictalurus punctatus*; cysts up to 3 mm. in diameter, conspicuous; spores, total length 60–70 μ , spore proper 18–20 μ by 4–5 μ wide by 3–3.5 μ thick.

H. mictospora Kudo. In urinary bladder of *Lepomis* spp. and *Micropterus salmoides*; spores 13.5–15 μ long, 8–9 μ wide, 6–7.5 μ thick; caudal prolongation 30–40 μ long.

Order 2 Actinomyxidia Stole

The Cnidosporidia placed in this order have been less frequently studied and, therefore, not so well known as the Myxosporidia. The spore is enveloped by a membrane, or shell composed of 3 valves which are sometimes drawn out into simple or bifurcated processes. There are also 3 polar capsules in the spore and the polar filaments are plainly visible *in vivo*. One to several sporoplasms occur in each spore. In the fully grown stage, the body is covered by a membrane and contains always 8 sporoplasts which

develop in turn into 8 spores. Whether the pansporoblast is formed by the union of 2 cells or not, is yet to be confirmed. The nuclei and cytoplasm divide and isogamy takes place. The zygote thus formed is the sporont, from which a single spore is produced by repeated nuclear division combined with cytoplasmic differentiation.

The Actinomyxidia inhabit the body cavity or the gut-epithelium of fresh or salt water annelids.

Spore with a double membrane; inner membrane a single piece, the outer trivalve; a single binucleate sporoplasm

..... Family 1 Tetractinomyxidae

Spore membrane a single trivalve shell; a single octonucleate sporoplasm or 8 uninucleate sporoplasms.....

..... Family 2 Triactinomyxidae

Family 1 Tetractinomyxidae Poche

Genus **Tetractinomyxon** Ikeda. In coelom of the sipunculid *Petalostoma minutum*; spores tetrahedron, without processes; trophozoite a rounded body, when mature; pansporoblast develops 8 spores. Seemingly borderline forms between the Myxosporidia and the Actinomyxidia.

T. intermedium I. (Fig. 217, a). Spherical pansporoblasts 20–25 μ in diameter; spores 7–8 μ in diameter; in coelom of the sipunculid, *Petalostoma minutum*.

Family 2 Triactinomyxidae

Genus **Triactinomyxon** Stole. Each of 3 shell-valves drawn out into a long process, the whole anchor-like; spore with 8 or more uninucleate sporoplasms; in gut-epithelium of oligochaetes.

T. ignotum S. (Fig. 217, d). Spore with 8 sporoplasms; in *Tubifex tubifex*.

T. magnum Granata. Spore with 16 sporoplasms; in *Limnodrilus udekemianus*.

T. legeri Mackinnon et Adams. Spore with 24 sporoplasms; in *Tubifex tubifex*.

T. dubium G. Spore with 32 sporoplasms; in *Tubifex tubifex*.

T. mrazeki M. et A. Spore with 50 sporoplasms; in *Tubifex tubifex*.

Genus **Sphaeractinomyxon** Caullery et Mesnil. In coelom of oligochaetes; spores rounded, without any processes; in early stage of development, there are 2 uninucleate bodies surrounded

by a binucleate envelope; 2 inner cells multiply into 16 cells which unite in pairs; nucleus of zygote or sporont divides first into 2; 1 of the nuclei divides into 6 which form 3 shell-valves and 3 polar capsules, while the other nucleus together with a portion of cyto-

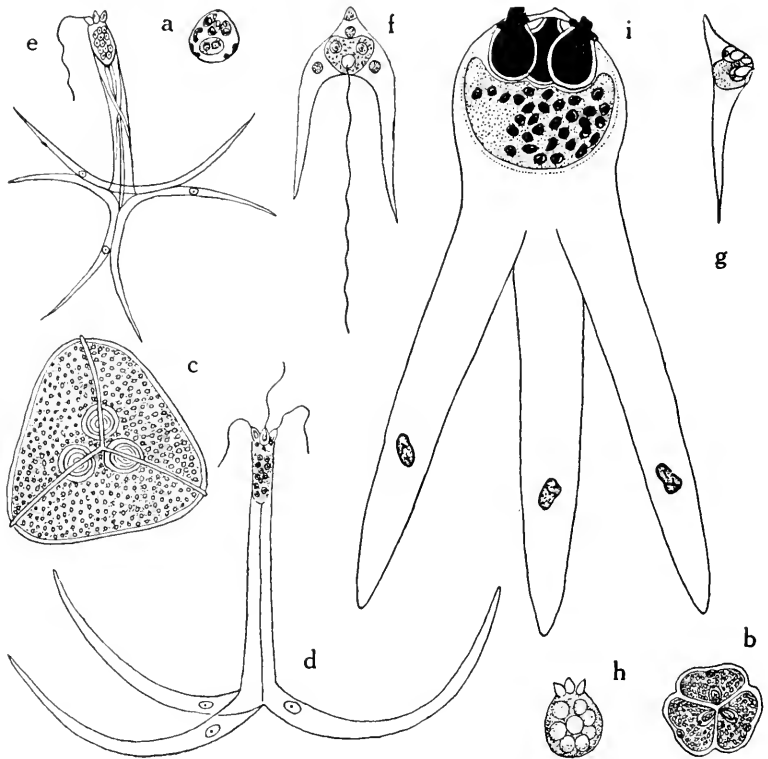


FIG. 217. a, *Tetractinomyxon intermedium*, $\times 800$ (Ikeda); b, *Sphaeractinomyxon stolci*, $\times 600$ (Caullery and Mesnil); c, *S. gigas*, $\times 665$ (Granata); d, *Triactinomyxon ignotum*, $\times 165$ (Léger); e, *Hexactinomyxon psammoryctis*, $\times 300$ (Stole); f, g, *Synactinomyxon tubificis*, $\times 600$ (Stole); h, *Neoactinomyxum globosum*, $\times 860$ (Granata); i, *Guyenotia sphaerulosa*, $\times 2095$ (Naville).

plasm remains outside the envelope, and undergoes multiplication; multinucleate sporoplasm migrates into spore; sporoplasm later divides into a large number of uninucleate sporoplasms which, when spores gain entrance into a new host, begin development.

S. stolei C. et M. (Fig. 217, *b*). Spore spherical; in *Clitellis arenarius* and *Hemitubifex benedii*.

S. gigas Granata (Fig. 217, *c*). In coelom of *Limnodrilus hoffmeisteri*.

Genus **Hexactinomyxon** Stole. Each of 3 shell-valves prolonged into 2 processes; spore appears as a 6-armed anchor.

H. psammoryctis S. (Fig. 217, *e*). In gut-epithelium of *Psammoryctes barbatus*; sporoplasm multinucleate.

Genus **Synactinomyxon** Stole. Spore with 2 prolonged shell-valves and 1 conical valve.

S. tubificis S. (Fig. 217, *f, g*). In gut-epithelium of *Tubifex tubifex*.

Genus **Neoactinomyxum** Granata. 3 shell-valves without any process, distended to hemisphere.

N. globosum G. (Fig. 217, *h*). In gut-epithelium of *Limnodrilus udekemianus*; spore with numerous sporoplasms.

Genus **Guyenotia** Naville. Pansporoblast with 8 spores; spore spherical with 3 shell-valves, each drawn out into digitiform process posteriorly, longer than diameter of spore; sporoplasm with 32 nuclei.

G. sphaerulosa N. (Fig. 217, *i*). In gut-epithelium of *Tubifex tubifex*; spores 15μ in diameter; appendages of mature spore 40μ long.

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Order 3 Microsporidia Balbian

THE Microsporidia are far more widely distributed as parasites among various animal phyla than are the Myxosporidia. They are, however, typically parasites of arthropods and fishes. Aside from 1 or 2 species, all Microsporidia invade and destroy host cells. Frequently these infected cells may show enormous hypertrophy of both the cytoplasmic body and the nuclei (Fig. 218), a characteristic feature of the host reaction toward this particular group of protozoan parasites.

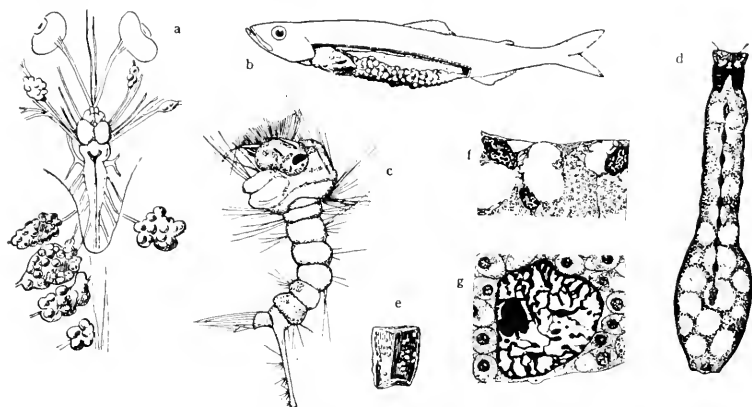


FIG. 218. Effects of microsporidian infection upon hosts. a, the central nervous system of *Lophius piscatoris* infected by *Nosema lophii* (Doflein); b, a smelt infected by *Glugea hertwigi* (Schrader); c, larva of *Culex territans* infected by *Thelohania opacita*, $\times 10$ (Kudo); d, a *Simulium* larva infected by *T. multispora*, $\times 8$ (Strickland); e, part of testis of *Barbus barbus* infected by *Plistophora longifilis*, $\times 1$ (Schuberg); f, g, normal and hypertrophied nucleus of adipose tissue of larval *Culex pipiens*, the latter due to infection by *Stempellia magna*, $\times 1000$ (Kudo).

The microsporidian **spore** is relatively small. In the vast majority it measures $3-6\mu$ long. The spore **membrane**, which is apparently of a single piece, envelops the **sporoplasm** and the **polar filament**, a very long and fine filament. The latter may directly be coiled in the spore or may be encased within a polar capsule which is similar to that of a myxosporidian or actinomyxidian

spore in structure, but which is mostly obscure *in vivo*, because of the minuteness of the object.

When such spores are taken into the digestive tract of a specific host (Fig. 219), the polar filaments are extruded and perhaps anchor the spores to the gut-epithelium. The sporoplasms emerge through the opening after the filaments become completely detached. By amoeboid movements they penetrate through the intestinal epithelium and enter the blood stream or body cavity and reach their specific site of infection. They then enter the host cells and undergo schizogonic multiplication at the expense of the

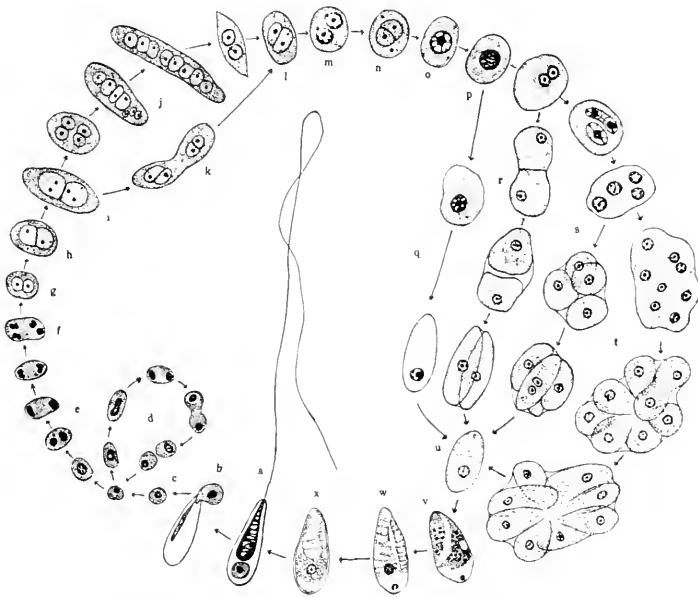


FIG. 219. The life-cycle of *Stempellia magna*, $\times 800$ (Kudo). a, b, germination of spore in the mid-gut of culicine larva; c-k, schizogony; l-p, sporont formation; q-t, formation of 1, 2, 4, and 8 sporoblasts; u, sporoblast; v-x, development of sporoblast into spore.

latter. The **schizonts** become **sporonts**, each of which produces a number of spores characteristic of each genus. Some spores seem to be capable of germinating in the same host body, and thus the number of infected cells increases. When heavily infected, the host animal dies as a result of the degeneration of enormous numbers of cells thus attacked. Such fatal infections may occur in an epidemic form, as is well known in the case of the pébrine disease

of silkworms, the nosema-disease of honey bees, microsporidiosis of mosquito larvae, etc.

Spore with a single polar filament.....Suborder 1 Monocnidea
 Spore with 2 polar filaments.....Suborder 2 Dienidea (p. 478)

Suborder 1 **Monocnidea** Léger et Hesse

Spore oval, ovoid, or pyriform; if subcylindrical length less than 4 times breadth.....Family 1 Nosematidae

Spore spherical or subspherical.....Family 2 Coccosporidae (p. 477)

Spore tubular or cylindrical, width less than $1/5$ length; straight or curved.....Family 3 Mrazekiidae (p. 477)

Family 1 **Nosematidae** Labbé

The majority of Microsporidia belong to this family.

Genus **Nosema** Nägeli. Each sporont develops into a single spore. Numerous species.

N. bombycis N. (Fig. 220, a, b). In all tissues of embryo, larva, pupa and adult of *Bombyx mori*; spores $3-4\mu$ by $1.5-2\mu$, polar filament $57-72\mu$ long; the causative organism of the pébrine disease of the silkworm.

N. bryozoides (Korotneff) (Fig. 220, c, d). In germ cells and cavity of *Plumatella fungosa* and *P. repens*; spores $7-10\mu$ by $5-6\mu$.

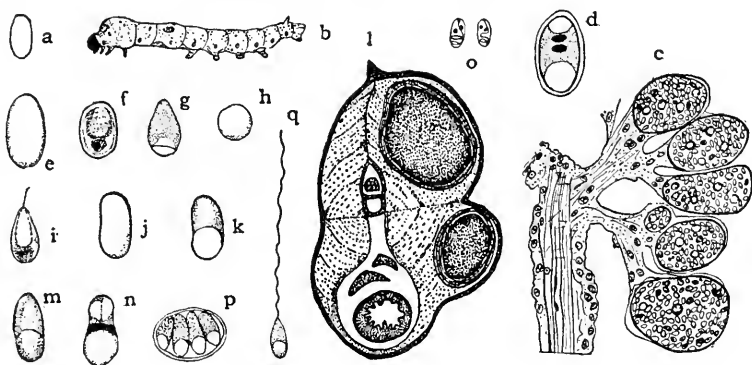


FIG. 220. a, b, *Nosema bombycis* (a, spore, $\times 1470$; b, an infected silk-worm larva, $\times 3$) (Kudo); c, d, *N. bryozoides* (c, infected funiculus, $\times 270$ (Braem); d, a spore, $\times 1200$ (Schröder)); e, f, *N. apis*, $\times 1560$ (Kudo); g-i, *N. cyclopis*, $\times 1560$ (Kudo); j, k, *N. anophelis*, $\times 1600$ (Kudo); l, m, *Glugca anomala* (l, section of an infected *Gasterosteus aculeatus* (Thélohan); m, a spore, $\times 1500$ (Stempell)); n, *G. hertwigi*, $\times 1670$ (Weissenberg); o, *Perezia mesnili*, $\times 800$ (Paillot); p, q, *Gurleya richardi*, $\times 1200$ (Cépède).

N. apis Zander (Fig. 220, *e, f*). In gut of honey bees; spores $4-6\mu$ by $2-4\mu$.

N. cyclopis Kudo (Fig. 220, *g-i*). In *Cyclops fuscus*; spores 4.5μ by 3μ .

N. anophelis K. (Fig. 220, *j, k*). In *Anopheles quadrimaculatus* (larva); spores $5-6\mu$ by $2-3\mu$.

Genus **Glugea** Thélohan. Each sporont develops into 2 spores; the infected host cells become extremely hypertrophied, and transform themselves into the so-called **Glugea cysts**. Many species.

G. anomala (Moniez) (Fig. 220, *l, m*). In connective tissue of stickle backs; spores $4-6\mu$ by $2-3\mu$.

G. mulleri Pfeiffer. In muscles of Gammarus; spores $5-6\mu$ by $2-3\mu$.

G. hertwigi Weissenberg (Figs. 218, *b*; 220, *n*). In various tissue cells of Osmerus; spores $4-5.5\mu$ by $2-2.5\mu$.

Genus **Perezia** Léger et Duboseq. Each sporont produces 2 spores as in Glugea, but infected host cells are not hypertrophied. A few species.

P. mesnili Paillot (Fig. 220, *o*). In cells of silk glands and Malpighian tubules of larvae of *Pieris brassicae*; spores 3.4μ by $1.5-2\mu$.

Genus **Gurleya** Doflein. Each sporont develops into 4 sporoblasts and finally into 4 spores. Not common.

G. richardi Cépède (Fig. 220, *p, q*). In *Diaptomus castor*; spores $4-6\mu$ by 2.8μ .

Genus **Thelohania** Henneguy. Each sporont develops into 8 sporoblasts and ultimately into 8 spores; sporont membrane may degenerate at different times during spore formation. Numerous species.

T. legeri Hesse (Figs. 68; 221, *a-e*). In fat-bodies of anopheline larvae; spores $4-6\mu$ by $3-4\mu$; heavily infected larvae die without metamorphosing into adults; widely distributed.

T. opacita Kudo (Figs. 218, *c*; 221, *f-h*). In fat-bodies of culicine larvae; spores $5.5-6\mu$ by $3.5-4\mu$.

Genus **Stempellia** Léger et Hesse. Each sporont produces 1, 2, 4, or 8 sporoblasts and finally 1, 2, 4, or 8 spores. 2 species.

S. magna Kudo (Figs. 218, *f, g*; 219; 221, *i-l*). In fat-bodies of various culicine larvae; spores $12.5-16.5\mu$ by $4-5\mu$; polar capsule visible in life; polar filament when extruded under mechanical pressure, measures up to $350-400\mu$ long.

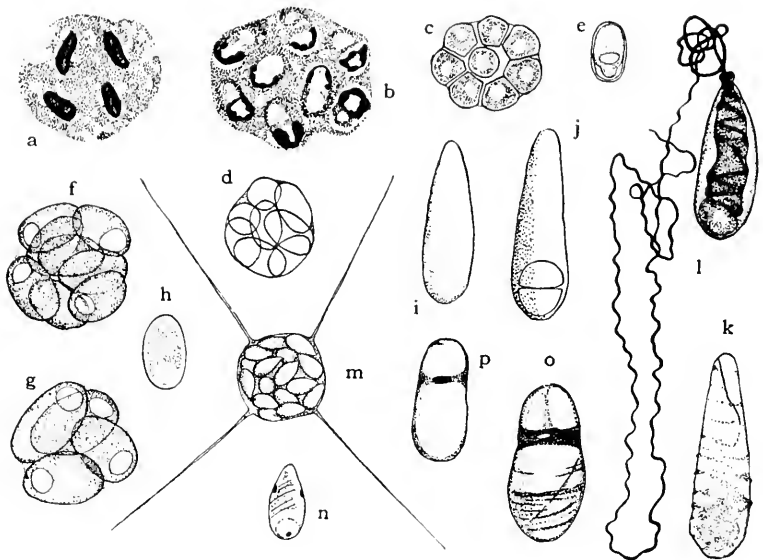


FIG. 221. a-e, *Thelohanía legeri* (a, b, sporogony; c, d, mature pansporoblasts; e, a spore), $\times 1570$ (Kudo); f-h, *T. opacita* (f, g, octosporous and tetrasporous pansporoblasts; h, a spore), $\times 1570$ (Kudo); i-l, *Stempellia magna* (i-k, spores; l, a spore with the extruded polar filament), $\times 1570$ (Kudo); m, n, *Trichoduboscquia epeori* (m, pansporoblast with mature spores, $\times 1330$; n, a spore, $\times 2670$) (Léger); o, p, *Plistophora longifilis* (Schuberg).

Genus **Duboscquia** Pérez. Sporont develops into 16 sporoblasts and finally 16 spores. One species.

D. legeri P. In body cavity of *Reticulitermes lucifugus*; spores 5μ by 2.5μ .

Genus **Trichoduboscquia** Léger. Similar to *Duboscquia* in number of spores produced from each sporont; but spore with 4 (or 3) rigid transparent prolongations of shell, difficult to see in life. One species.

T. epeori L. (Fig. 221, m, n). In fat-bodies of nymphs of *Epeorus torrentium* and *Rhithrogena semicolorata*; sporonts spherical, $9-10\mu$ in diameter, with usually 16 spores; prolongations of shell, $20-22\mu$ long; spores pyriform, $3.5-4\mu$ long.

Genus **Plistophora** Gurley. Sporont develops into variable number of (often more than 16) sporoblasts, each of which becomes a spore. Several species.

P. simulii (Lutz et Splendore). In larvae of *Simulium* spp.; spores $4.5\text{--}8\mu$ by 3.5μ .

P. longifilis Schuberg (Figs. 218, *e*; 221, *o*, *p*). In testis of *Barbus fluviatilis*; spores 3μ by 2μ up to 12μ by 6μ ; extruded polar filaments up to 510μ long.

Genus **Pyrotheca** Hesse. Schizogony and sporogony unknown; spores elongate pyriform, anterior end attenuated, posterior end rounded, slightly curved; sporoplasm in posterior region, with 1–2 nuclei; polar capsule large. One species.

P. incurvata H. (Fig. 222, *a*, *b*). In fat-bodies and haemocoel of *Megacyclops viridis*; spores 14μ by 3μ ; polar filament 130μ long.

Family 2 Coccosporidae Kudo

Genus **Coccospora** Kudo (*Cocconema* Léger et Hesse). Spore spherical or subspherical. Several species.

C. slavinae (L. et H) (Fig. 222, *c*, *d*). In gut-epithelium of *Slavina appendiculata*; spores about 3μ in diameter.

Family 3 Mrazekiidae Léger et Hesse

Genus **Mrazekia** L. et H. Spore straight, tubular; long or short process at one extremity.

M. caudata L. et H. (Fig. 222, *e*, *f*). In lymphocytes of *Limnodrilus* and *Tubifex*; spores $16\text{--}18\mu$ by $1.3\text{--}1.4\mu$.

Genus **Bacillidium** Janda. Spore cylindrical, without any process; one end narrowed in a few species. 8 species.

B. limnodrili Jirovec (Fig. 222, *g*). In lymphocytes within gonads of *Limnodrilus claparedeanus* in Bohemia; spores $22\text{--}24\mu$ by 1.5μ .

Genus **Cougourdella** Hesse. Spore cylindrical, with an enlarged extremity, resembling fruit of *Lagenaria cougourda*. 3 species.

C. magna H. (Fig. 222, *h*, *i*). In haemocoel and fat body of *Megacyclops viridis*; spores 18μ by 3μ ; polar filament 110μ long; sporoplasm with 1–2 nuclei or 2 uninucleate sporoplasms.

Genus **Octosporea** Flu. Spore cylindrical; more or less curved; ends similar. 2 species.

O. muscae-domesticae F. (Fig. 222, *j*). In gut and germ cells of *Musca* and *Drosophila*; spores $5\text{--}8\mu$ long.

Genus **Spiroglugea** Léger et Hesse. Spore tubular and spirally curved; polar capsule large. One species.

S. octospora L. et H. (Fig. 222, *k*, *l*). In fat body of larvae of *Ceratopogon* sp.; spores $8\text{--}8.5\mu$ by 1μ .

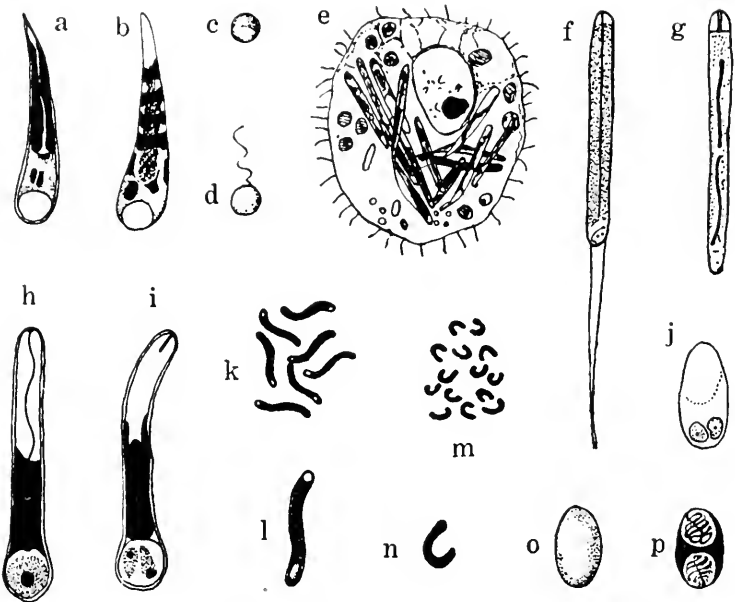


FIG. 222. a, b, *Pyrotheca incurvata*, $\times 2000$ (Hesse); c, d, *Coccospora slaviniae* (d, with extruded polar filament), $\times 2000$ (Léger and Hesse); e, f, *Mrazekia caudata* (e, an infected host cell, $\times 700$ (Mrazek); f, a spore, $\times 1750$ (Léger and Hesse)); g, *Bacillidium limnodrili*, $\times 1400$ (Jírovec); h, i, *Cougourdella magna*, $\times 2000$ (Hesse); j, *Octosporea muscae-domesticae*, $\times 2150$ (Chatton and Krempf); k, l, *Spiroglugea octospora* (k, $\times 1000$; l, $\times 3000$) (Léger and Hesse); m, n, *Toxoglugea vibrio* (m, $\times 1000$; n, $\times 3000$) (Léger and Hesse); o, p, *Telomyxa glugeiformis*, $\times 3000$ (Léger and Hesse).

Genus **Toxoglugea** Léger et Hesse. Minute spore curved or arched in semi-circle. One species.

T. vibrio L. et H. (Fig. 222, m, n). In fat body of *Ceratopogon* sp.; spores 3.5μ by less than 0.3μ .

Suborder 2 Dicnidea Léger et Hesse

Family Telomyxidae Léger et Hesse

Genus **Telomyxa** Léger et Hesse. Spore with 2 polar capsules; sporont develops into 8, 16, or more sporoblasts and finally 8, 16, or more spores. One species.

T. glugeiformis L. et H. (Fig. 222, o, p). In fat body of larva of *Ephemera vulgata*; spores 6.5μ by 4μ .

Order 4 **Helicosporidia** Kudo

This order has been created to include the interesting organism, *Helicosporidium*, observed by Keilin. Although quite peculiar in the structure of its spore, the organism seems to be best placed in the Cnidosporidia, if it is a protozoan.

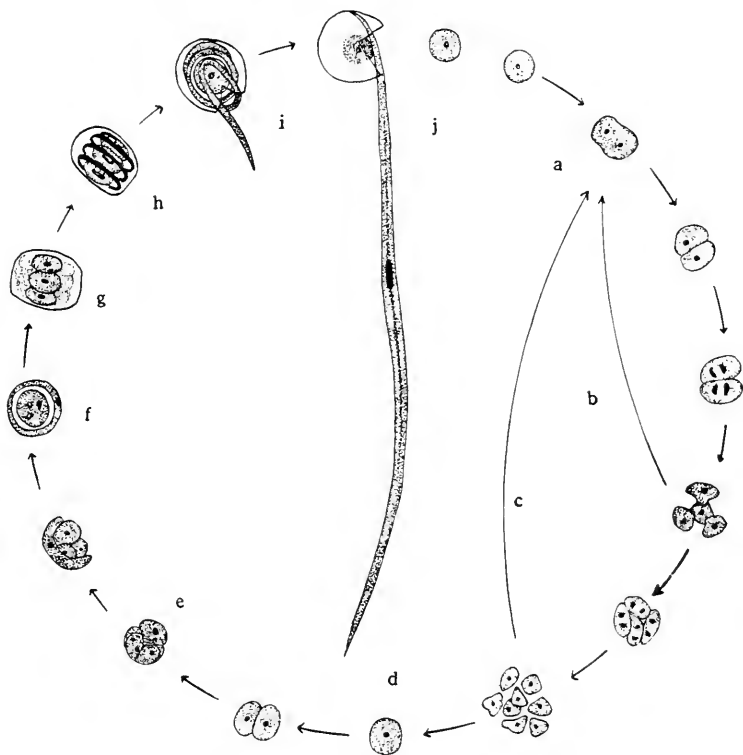


FIG. 223. Diagram illustrating the probable development of *Helicosporidia*, \times about 1600 (Keilin). a-c, schizont and schizogony; d, sporont(?); e, three stages in formation of four-celled stage; f, hypothetical stage; g, young spore before the spiral filament is formed; h, mature spore; i, j, opening of spore and liberation of sporozoites. a-h, in living host larva; i, j, in dead host body.

The minute spore is composed of a thin membrane of one piece and of three uninucleate sporoplasms, around which is coiled a long thick filament. Young trophozoites are found in the host tissues or body cavity. They undergo schizogony, at the end of which uninucleate sporonts become differentiated. A sporont

divides apparently twice and thus forms four small cells which develop into a spore. The complete life-history is still unknown.

Genus **Helicosporidium** Keilin. Parasitic in insects; schizogony and sporogony; spore with central sporoplasms and a single thick coiled filament. One species.

H. parasiticum K. (Fig. 223). In body cavity, fat body, and nervous system of larvae of *Dasyhelea obscura* and *Mycetobia palipes* (Diptera), and *Hericia hericia* (Acarina), all of which inhabit wounds of elm and horse-chestnut trees; schizonts minute; spores 5–6 μ in diameter; extruded filament 60–65 μ by 1 μ thick.

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CHAPTER 29

Subphylum 2 **Ciliophora** Doflein

THE Ciliophora possess cilia which serve as cell-organs of locomotion and food-capture. In Suctorioria the cilia are present only during early developmental stages. The members of this subphylum possess a unique organization not seen in the Plasmodroma; namely, except Protociliata, the Ciliophora contain two kinds of nuclei, the macronucleus and the micronucleus. The former is large and massive, and controls the metabolic activities of the organism, while the latter is minute and usually vesicular or less compact, and is concerned with the reproductive processes. Nutrition is holozoic or parasitic; holophytic in a few forms. Sexual reproduction is mainly by conjugation, and asexual reproduction is by binary fission or budding. The majority are free-living, but a number of parasitic forms also occur.

The Ciliophora are divided into two classes:

Cilia present throughout trophic life Class 1 Ciliata
Adult with tentacles; cilia only while young
. Class 2 Suctorioria (p. 628)

Class 1 **Ciliata** Perty

The class Ciliata includes Protozoa of various habitats and body structures, though all possess cilia or cirri during the trophic stage of life. They inhabit all sorts of fresh and salt water bodies by free-swimming, creeping, or being attached to other objects; some are endozoic in other animals. Free-swimming forms are usually spherical to elliptical, while the creeping forms are, as a rule, flattened or compressed.

The cilia are extremely fine, comparatively short, and as a rule arranged in rows. In some forms they diminish in number and are replaced by cirri. The cilia are primarily cell-organs of locomotion, but secondarily through their movements bring the food matter into the cytostome. Moreover, certain cilia appear to be tactile organellae. The food of free-living ciliates consists of small plant and animal organisms which ordinarily abound in the water; thus their nutrition is holozoic. The ciliates vary in size from less than 10μ up to 2 mm. in large forms (as in an extended

Spirostomum or Stentor). The cytoplasm is distinctly differentiated into the ectoplasm and the endoplasm. The ectoplasm gives rise to the cilia and trichocysts and is covered by a pellicle. The endoplasm contains nuclei, food vacuoles, contractile vacuoles, pigment granules, crystals, etc. In the majority of ciliates, the anterior and posterior extremities are permanent and distinct; in all cytostome-possessing forms, the oral and aboral surfaces are distinguishable, while in numerous creeping forms the dorsal and ventral sides are differentiated.

The body is covered by a very thin yet definite membrane, the pellicle, which is ordinarily uniformly thin and covers the entire body surface so closely that it is not recognizable in life. In some forms, such as *Coleps*, it develops into numerous platelets and in others, such as *Trichodina*, into hook-like processes. The outer half of the ectoplasm may show alveolar structure which, in section, exhibits radiating and parallel lines. In this portion the myonemes (p. 51) are lodged. The deeper layer of the ectoplasm is structureless and free from granules. In the ectoplasm are embedded the basal granules of cilia, which are arranged in longitudinal, oblique, or spiral rows. In recent years complex fibrillar systems have been recognized in many ciliates (p. 55-59). The cilia may fuse to form cirri, membranellae, and undulating membranes which occur in certain groups. In many euciliates contractile vacuoles with one to several collecting canals are one of the prominent structures. The endoplasm is more fluid and the ground substance is finely granulated or reticulated; it undergoes rotation movement or cyclosis.

Two types of nuclei are present in all euciliates. The massive macronucleus is of various forms. The chromatin granules which may reach 20μ in diameter (p. 34) fill compactly the intranuclear space. The macronucleus multiplies by amitosis. The micronucleus is ordinarily so minute that it is difficult to see in a living specimen. It is vesicular in structure, although in some it appears to be compact, and consists of an endosome, the nucleoplasm, and the membrane. The number of micronuclei present in an individual varies among different species. At the time of reproduction it increases in size and divides mitotically; during conjugation it undergoes a meiotic division (p. 158).

The protociliates possess from one to many hundreds of nuclei of a uniformly same structure and numerous ovoid or spindle-

shaped bodies, the nature of which is open to speculation. Some authors think that they are nuclei—micronuclei (after Hickson) or macronuclei (after Konsuloff). Metcalf considers that each nucleus possesses both metabolic chromatin and reproductive chromatin, the former being seen as large flattened peripheral masses and the latter, as smaller spheroidal granules.

In all except protociliates and a comparatively small number of astomous euciliates, there is a cytostome which in its simplest form is represented by a small opening on the pellicle, and may or may not be closed when the animal is not feeding. The cytostome opens into the cytopharynx (or gullet), a canal which ends in the deeper portion of the endoplasm. In the cytopharynx there may be present one or more undulating membranes to facilitate intaking of the food. Occasionally the cytostome is surrounded by trichites or trichocysts (p. 62). When the cytostome is not at the anterior region as, for instance, in *Paramecium*, there is a peristome (or oral groove) which starts at or near the anterior end and runs posteriorly. The peristome is ciliated so that food particles are thrown down along it and ultimately into the cytostome which is located at its posterior end. Solid waste particles are extruded from the cytopyge, or cell-anus, which is usually noticeable only at the time of actual defecation (p. 92).

Following Metcalf, Ciliata are here divided into 2 subclasses:
 2-many nuclei of one kind; sexual reproduction permanent fusion . . .
 Subclass 1 Protociliata
 Macronucleus and micronucleus; sexual reproduction conjugation . . .
 Subclass 2 Euciliata (p. 487)

Subclass 1 **Protociliata** Metcalf

The protociliates are exclusively inhabitants of the intestine of Anura, excepting 3 species, 2 of which occur in Urodeles and one in a marine fish. The body is covered uniformly by cilia of equal length. There is no cytostome and the nutrition is parasitic (saprozoic). The number of nuclei varies from 2 to several hundreds, all of which are of one type. Asexual reproduction is by binary fission. In a number of species sexual fusion of 2 gametes has been observed (Fig. 225, *a-d*). Encystment is common. One family.

Family **Opalinidae** Claus

Genus **Opalina** Purkinje et Valentin. Highly flattened; multinucleate; in amphibians. Numerous species.

O. hylaxena Metcalf (Fig. 224, a). In *Hyla versicolor*; larger individuals about 420μ long, 125μ wide, 28μ thick. Several subspecies (Metcalf).

O. obtrigonoidea M. (Fig. 224, b-f). $400\text{--}840\mu$ long, $175\text{--}180\mu$ wide, $20\text{--}25\mu$ thick; in various species of frogs and toads (*Rana*, *Hyla*, *Bufo*, *Gastrophryne*, etc.), North America. Numerous subspecies (Metcalf).

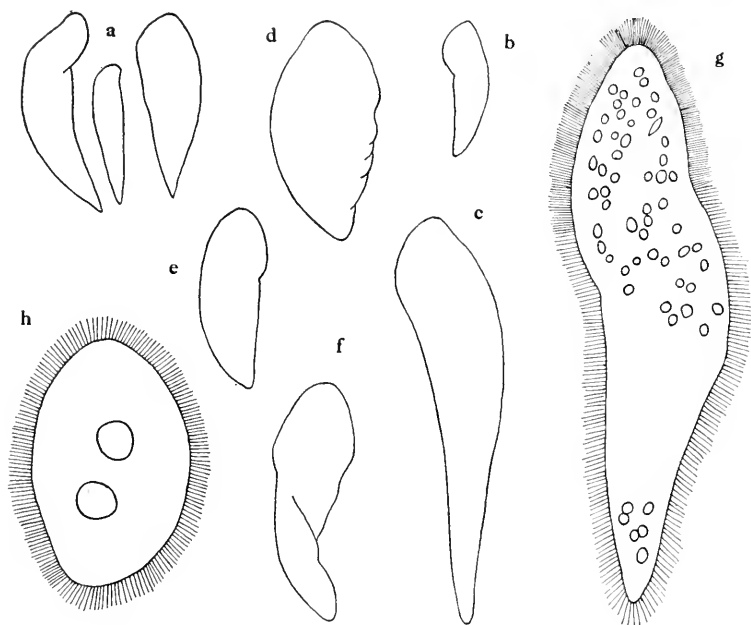


FIG. 224. a, 3 individuals of *Opalina hylaxena*, $\times 230$; b-f, *O. obtrigonoidea*, $\times 60$ (b, c, from *Bufo fowleri*; d-f, from *Rana pipiens*); g, *Cepedea cantabrigensis*, $\times 230$; h, *Zelleriella scaphiopodos*, $\times 230$. (All after Metcalf.)

O. carolinensis M. $90\text{--}400\mu$ by $32\text{--}170\mu$; in *Rana pipiens sphenoccephala*.

O. pickeringii M. $200\text{--}333\mu$ by $68\text{--}100\mu$; in *Hyla pickeringii*.

O. oregonensis M. 526μ by 123μ ; in *Hyla regilla*.

O. spiralis M. $300\text{--}355\mu$ long, $130\text{--}140\mu$ wide, $25\text{--}42\mu$ thick; in *Bufo compactilis*.

O. chorophili M. About 470μ by 100μ ; in *Chorophilus triseriatus*.

O. kennicotti M. About 240μ by 85μ ; in *Rana areolata*.

Genus **Cepedea** Metcalf. Cylindrical or pyriform; circular in cross-section; multinucleate; all in Amphibia. Numerous species.

C. cantabrigensis M. (Fig. 224, g). About 350μ by 84μ ; in *Rana cantabrigensis*.

C. hawaiiensis M. $170\text{--}200\mu$ by $43\text{--}60\mu$; in *Rana catesbeiana*; Hawaii.

C. obovoidea M. About 315μ by 98μ ; in *Bufo lentiginosus*.

C. floridensis M. About 230μ by 89μ ; in *Scaphiopus albus*.

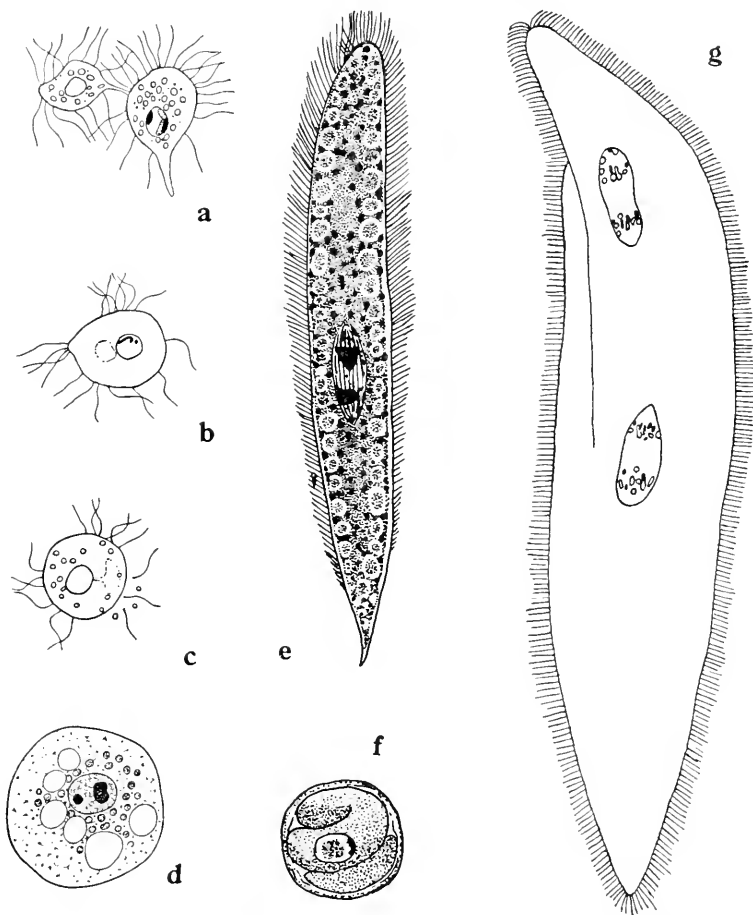


FIG. 225. a-d, stages in sexual reproduction in *Protoopalina intestinalis* (Metcalf); e, f, *P. saturnalis*, $\times 500$ (Léger and Duboscq); g, *P. mitotica*, $\times 380$ (Metcalf).

Genus **Protoopalina** Metcalf. Cylindrical or spindle-shaped, circular in cross-section; 2 nuclei; in rectum of various species of Amphibia with one exception. Numerous species.

P. intestinalis (Stein) (Fig. 225, *a-d*). About 330μ by 68μ ; in intestine of *Bombina bombina*, and *B. pachypa*, Europe.

P. saturnalis Léger et Duboseq (Fig. 225, *e, f*). In intestine of the marine fish, *Box boops*; $100-152\mu$ by $22-60\mu$.

P. mitotica (M.) (Fig. 225, *g*). 300μ by 37μ ; in intestine of *Ambystoma tigrinum*.

Genus **Zelleriella** Metcalf. Greatly flattened; 2 similar nuclei; all in Amphibia. Numerous species.

Z. scaphiopodos M. (Fig. 224, *h*). In *Scaphiopus solitarius*; about 150μ long, 90μ broad, 13μ thick.

Z. antilliensis (M.). About 180μ long, 113μ wide, 32μ thick; in *Bufo marinus*.

Z. hirsuta M. About 113μ long, 60μ wide, 22μ thick, in *Bufo cognatus*.

Z. intermedia M. (Fig. 61). About 94μ by 50μ by 16μ ; in *Bufo intermedicus* and *B. valliceps*.

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CHAPTER 30

Subclass 2 **Euciliata** Metcalf

THE most conspicuous group of Protozoa containing 2 nuclei: macronucleus and micronucleus. Sexual reproduction is through conjugation. We owe Kahl a great deal for his series of comprehensive taxonomic studies of free-living ciliates. The euciliates are grouped under the following four orders:

- Without adoral zone of membranellae. Order 1 Holotricha
- With adoral zone of membranellae
 - Adoral zone winds clockwise to cytostome
 - Peristome not extending beyond general body surface. Order 2 Spirotricha (p. 573)
 - Peristome extending out like funnel. Order 3 Chonotricha (p. 614)
 - Adoral zone winds counter-clockwise to cytostome. Order 4 Peritricha (p. 616)

Order 1 **Holotricha** Stein

The members of this order show uniform ciliation over the entire body surface. Adoral zone does not occur. The majority possess a cytostome, which varies among different forms. Nutrition is holozoic or saprozoic. Asexual reproduction is usually by transverse fission and sexual reproduction by conjugation. Encystment is common. The holotrichous ciliates are parasites or free-living in all sorts of fresh, brackish, and salt waters.

The order is here divided into 6 suborders:

- Without cytostome. Suborder 1 Astomata (p. 488)
- With cytostome
 - Cytostome not rosette-like
 - Without special thigmotactic ciliated field
 - Cytostome on body surface or in peristome, without strong cilia. Suborder 2 Gymnostomata (p. 496)
 - Cytostome in peristome, bearing special cilia or membranes
 - Peristome lined with rows of free cilia. Suborder 3 Trichostomata (p. 531)
 - Peristome with membrane; with or without free cilia. Suborder 4 Hymenostomata (p. 547)
 - With well-developed thigmotactic ciliated field; commensals in mussels. Suborder 5 Thigmatricha (p. 560)
 - Cytostome rosette-like small aperture or obscure; endoparasitic. Suborder 6 Apostomea (p. 567)

Suborder 1 **Astomata** Schewiakoff

The ciliates placed under this suborder possess no cytostome, although there may occur slit-like organella which has been looked upon as a vestigial cytostome. Of various forms and sizes, the body ciliation is uniform. Asexual division is carried on by transverse fission and often by budding which results in chain formation. Sexual reproduction is conjugation and in some encystment was noticed. These organisms are parasitic in various invertebrates in fresh or salt water.

Without attaching organellae or skeletal structures

Macronucleus round to elongate Family 1 Anoplophryidae

Macronucleus irregular network Family 2 Opalinopsidae (p. 491)

With attaching organellae or skeletal structures

Contractile vacuole, a long dorsal canal; usually with a sucking organella Family 3 Haptophryidae (p. 491)

Contractile vacuoles not canal-like; with various attaching organellae or skeletal structures
 Family 4 Intoshellinidae (p. 493)

Family 1 **Anoplophryidae** Cépède

Genus **Anoplophrya** Stein (*Collinia* Cépède). Oval, elongate, ellipsoid or cylindrical; macronucleus ovoid to cylindrical; micronucleus small; one to several contractile vacuoles; ciliation dense and uniform; in coelom and gut of Annelida and Crustacea. Numerous species.

A. marylandensis Conklin (Fig. 226, *a*). 36–72 μ by 16–42 μ ; in intestine of *Lumbricus terrestris* and *Helodrilus caliginosus*; Baltimore, Maryland.

A. orchestii Summers et Kidder (Fig. 226, *b*). Polymorphic according to size; pyriform to broadly ovoid; 7–45 ciliary rows meridional, unequally spaced, and more on one surface; macronucleus voluminous, a compact micronucleus; body 6–68 μ long; in the body of the sand-flea, *Orchestia agilis*; Woods Hole, Massachusetts. Summers and Kidder (1936) made careful observation on its conjugation and reorganization.

Genus **Rhizocaryum** Caullery et Mesnil. With hollowed ventral surface which serves for attachment; macronucleus drawn out like a tree-root. One species.

R. concavum C. et M. (Fig. 226, *c*). In gut of *Polydora caeca* and *P. flava* (polychaetes).

Genus **Metaphrya** Ikeda. Pyriform, anterior end bent slightly

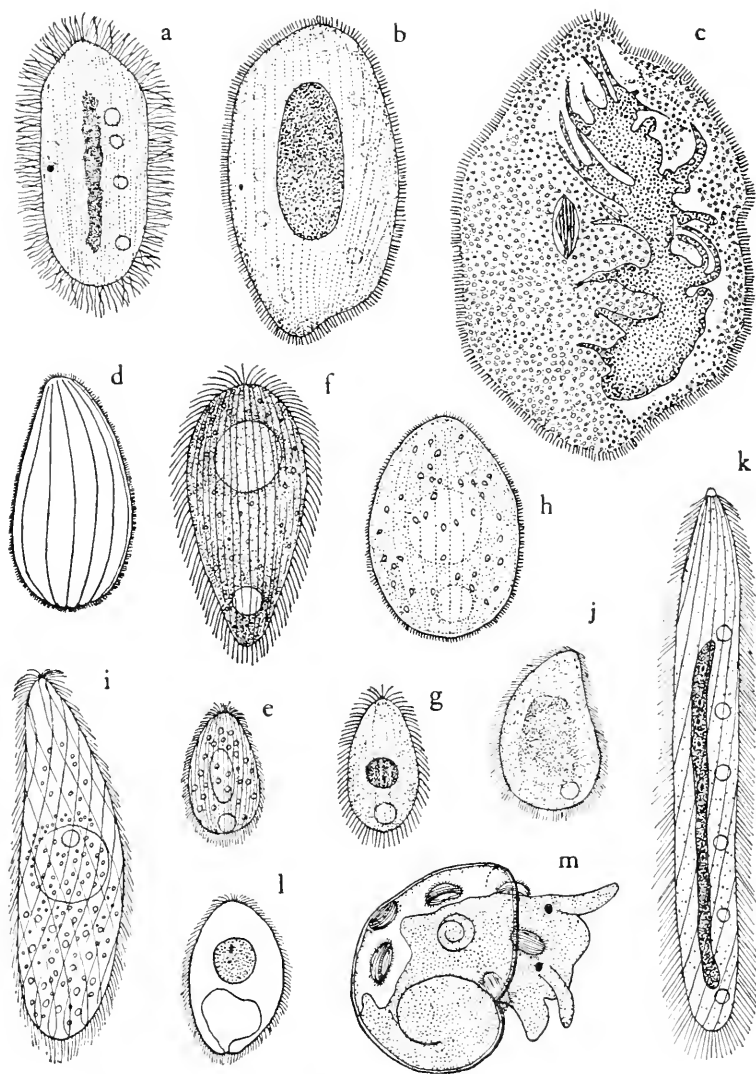


FIG. 226. a, *Anoplophrya marylandensis*, $\times 500$ (Conklin); b, *A. orchestii*, $\times 500$ (Summers and Kidder); c, *Rhizocaryum concavum*, $\times 670$ (Cépède); d, *Metaphrya sagittae*, $\times 120$ (Ikeda); e, *Perezella pelagica*, $\times 340$ (Cépède); f, *Dogielella sphaerii*, $\times 470$ (Poljansky); g, *D. minuta*, $\times 670$ (Poljansky); h, *D. virginia*, $\times 670$ (Kepner and Carroll); i, *Orchitophrya stellarum*, $\times 870$ (Cépède); j, *Kofoidella elutherae*, $\times 270$ (Cépède); k, *Butschliella opheliae*, $\times 350$ (Cépède); l, m, *Protophrya ovicola* (m, a young *Littorina rudis* with the ciliate, $\times 80$ (Cépède).

to one side; 12 longitudinal ciliary furrows; below ectoplasm, a layer of refringent material; endoplasm sparse; macronucleus basket-like, large, with a spacious hollow; a micronucleus; no contractile vacuoles. One species.

M. sagittae I. (Fig. 226, *d*). About 250μ by 130μ ; in the body-cavity of *Sagitta* sp.

Genus **Perezella** Cépède. Ovoid; ventral surface concave, serves for attachment; macronucleus ellipsoid; contractile vacuole terminal; longitudinally, uniformly, ciliated. A few species.

P. pelagica C. (Fig. 226, *e*). In coelom of copepods (*Ascartia*, *Clausia*, *Paracalanus*); about 48μ long.

Genus **Dogielella** Poljansky. Pyriform; longitudinal ciliary rows; contractile vacuole terminal; macronucleus spherical, with a spherical or elliptical micronucleus; in parenchyma of flat-worms or molluscs. 3 species.

D. sphaerii P. (Fig. 226, *f*). $40\text{--}100\mu$ by $25\text{--}54\mu$; in *Spacrium corneum*.

D. minuta P. (Fig. 226, *g*). $12\text{--}28\mu$ by up to 20μ ; in *Stenostomum leucops*.

D. virginia (Kepner et Carroll) (Fig. 226, *h*). $40\text{--}50\mu$ long; in the same host animal; Virginia.

Genus **Orchitophrya** Cépède. Elongate pyriform; ciliary rows oblique; macronucleus spherical, central. One species.

O. stellarum C. (Fig. 226, *i*). In gonads of the echinoderm, *Asteracanthion* (*Asterias*) *rubens*; $35\text{--}65\mu$ long.

Genus **Kofoidella** Cépède. Pyriform; macronucleus broadly oval; contractile vacuole, subterminal. One species.

K. eleutheriae C. (Fig. 226, *j*). In gastro-vascular cavity of the medusa, *Eleutheria dichotoma*; $30\text{--}80\mu$ long.

Genus **Herpetophrya** Siedlecki. Ovoid; with a pointed, mobile, tactile, non-ciliated cone; macronucleus globular; without contractile vacuole. One species.

H. astomata S. In coelom of Polymnia (annelid).

Genus **Butschliella** Awerinzew. Elongate with pointed anterior end, with non-ciliated retractile anterior cap; cilia in comparatively few (about 10) slightly spiral rows; macronucleus band-form; several contractile vacuoles in a longitudinal row. Several species.

B. opheliae A. (Fig. 226, *k*). In *Ophelia limacina*; $280\text{--}360\mu$ by $35\text{--}50\mu$.

B. chaetogastri Penard. Elongate lanceolate, slightly flattened; longitudinal rows of long cilia; cytoplasm colorless; macronucleus elongate; micronucleus voluminous, vesicular; without contractile vacuole; 60–120 μ long; in the oesophagus of *Chaetogaster* sp.

Genus **Cepedella** Poyarkoff. Pyriform with pointed anterior end, where there is a depression apparently used for fixation of body, from which longitudinal myonemes arise; macronucleus globular; without contractile vacuole. One species.

C. hepatica P. 16–26 μ long; intracellular parasite of liver of the cyclad mollusc, *Sphaerium corneum*.

Genus **Protophrya** Kofoid (*Isselina* Cépède). Ellipsoid to pyriform; spheroidal macronucleus; contractile vacuole terminal. 2 species.

P. ovicola K. (Fig. 226, *l, m*). About 60 μ long; in uterus of the mollusc, *Littorina rudis*.

Genus **Protanoplophrya** Miyashita. Similar to *Anoplophrya*; but with rudimentary oral apparatus, a long slit, an undulating membrane and cytopharynx in anterior region of body; macronucleus elongate band; numerous contractile vacuoles. One species.

P. stomata Miyashita (Fig. 227, *a*). Cylindrical; up to 1.5 mm. by about 70 μ ; in hind-gut of *Viviparus japonicus* and *V. malleatus*.

Family 2 Opalinopsidae Hartog

Genus **Opalinopsis** Foettinger. Oval or ellipsoid; macronucleus fragmented; ciliation uniform and close; parasite in liver of cephalopods. A few species.

O. sepiolae F. (Fig. 227, *b*). 40–80 μ long; in liver of *Sepiola rondelii* and *Octopus tetracirrhus*.

Genus **Chromidina** Gonder (*Benedenia* Foettinger). Elongate; anterior region broader, ends pointed; uniform ciliation; macronucleus in irregular network distributed throughout body; micronucleus obscure; budding and encystment; Cheissin holds that this is identical with *Opalinopsis*. One species.

C. elegans (Foettinger) (Fig. 227, *c, d*). 500–1500 μ by about 30–60 μ ; in kidney and gonad of cephalopods: *Sepia elegans*, *Loligo* sp., etc.

Family 3 Haptophryidae Cépède

Genus **Haptophrya** Stein. Elongate; uniformly ciliated; anterior end with a neck-like constriction; a circular sucker surrounded by 1–2 rows of cilia. A few species.

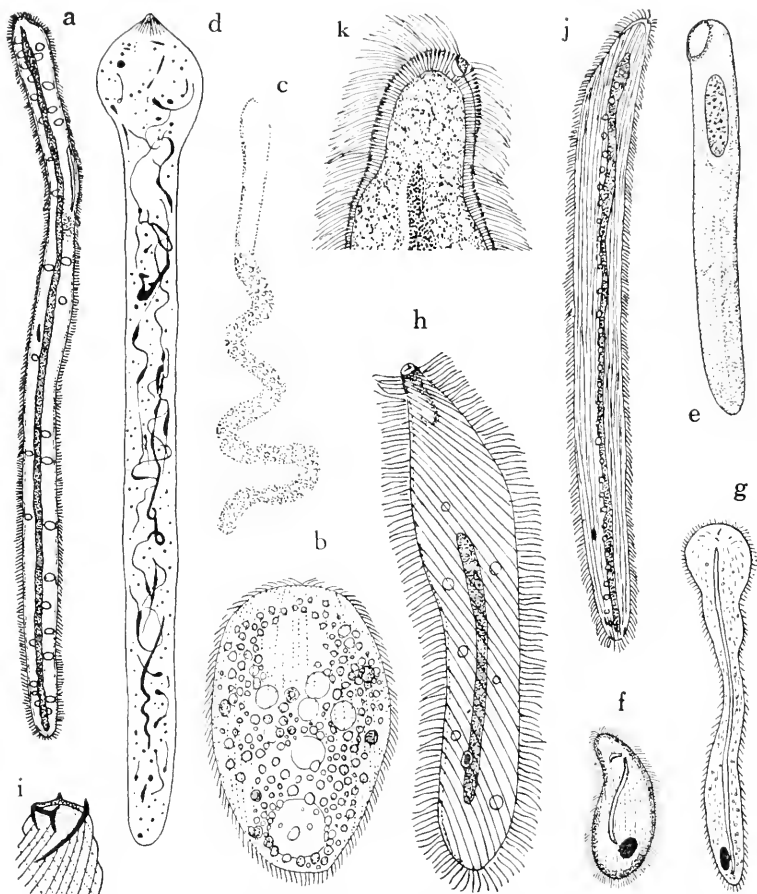


FIG. 227. a, *Protanoplophrya stomata*, $\times 100$ (Miyashita); b, *Opalinopsis sepiolae*, $\times 670$ (Gonder); c, d, *Chromidina elegans* (c, $\times 330$ (Chatton and Lwoff); d, $\times 220$ (Wermel)); e, *Haptophrya michiganensis*, $\times 35$ (Woodhead); f, *Lachmannella recurva*, $\times 100$ (Cépède); g, *Sieboldiellina planariarum*, $\times 100$ (Cépède); h, i, *Intoshellina poljanskyi* (h, $\times 300$; i, attaching organella seen from ventral side, $\times 870$) (Cheissin); j, k, *Monodontophrya kijenskiyi* (j, $\times 100$; k, anterior end in profile, $\times 870$) (Cheissin).

H. michiganensis Woodhead (Fig. 227, e). 1.1–1.6 mm. long; in gut of the four-toed salamander, *Hemidactylium scutatum*; Michigan.

Genus **Steinella** Cépède. Anterior end broad; sucker-like de-

pression without encircling cilia, but with 2 chitinous hooks. One species.

S. uncinata (Schultze). Up to 200μ long; in gastro-vascular cavity of *Planaria ulvae*, *Gunda segmentata* and *Proceros* sp.

Genus **Lachmannella** Cépède. With a chitinous hook at anterior end; elongate pyriform, anterior end curved; ciliation longitudinal and dense. One species.

L. recurva (Claparède et Lachmann) (Fig. 227, f). In gastro-vascular cavity of *Planaria limacina*; about 200μ long.

Genus **Sieboldiellina** Collin (*Discophrya* Stein). Vermiform, with neck-like constriction; simple sucker at anterior end. One species.

S. planariarum (Siebold) (Fig. 227, g). Up to 700μ long; in gastro-vascular cavity of various fresh- and salt-water turbellarians, most frequently *Planaria torva*.

Family 4 Intoshellinidae Cépède

Genus **Intoshellina** Cépède. Elongate; ciliary rows slightly spiral; macronucleus voluminous, highly elongate; 5–7 contractile vacuoles scattered in posterior region; a complicated attaching organella at anterior end (Fig. 227, i); vestigial cytopharynx.

I. poljanskyi Cheissin (Fig. 227, h, i). $170\text{--}280\mu$ long; in intestine of *Limnodrilus arenarius*.

Genus **Monodontophrya** Vejdowsky. Elongate; anterior end with thick ectoplasm; attaching organella at anterior end, with fibrils; macronucleus elongate; contractile vacuoles, numerous in a longitudinal row.

M. kijenskiyi Cheissin (Fig. 227, j, k). $400\text{--}800\mu$ long; in anterior portion of intestine of *Tubifex inflatus*.

Genus **Maupasella** Cépède. Ellipsoid; close longitudinal ciliary rows; with a spinous attaching organella at anterior end, with fibrils; contractile vacuoles in 2 irregular rows; macronucleus elongate. One species.

M. nova C. (Fig. 228, a). $70\text{--}130\mu$ long; in intestine of *Allolobophora caliginosa* (annelid).

Genus **Schultzellina** Cépède. Similar to *Maupasella*; but with attaching organella set obliquely; macronucleus voluminous, reniform.

S. mucronata C. (Fig. 228, b). In intestine of *Allurus tetraedurus* (annelid).

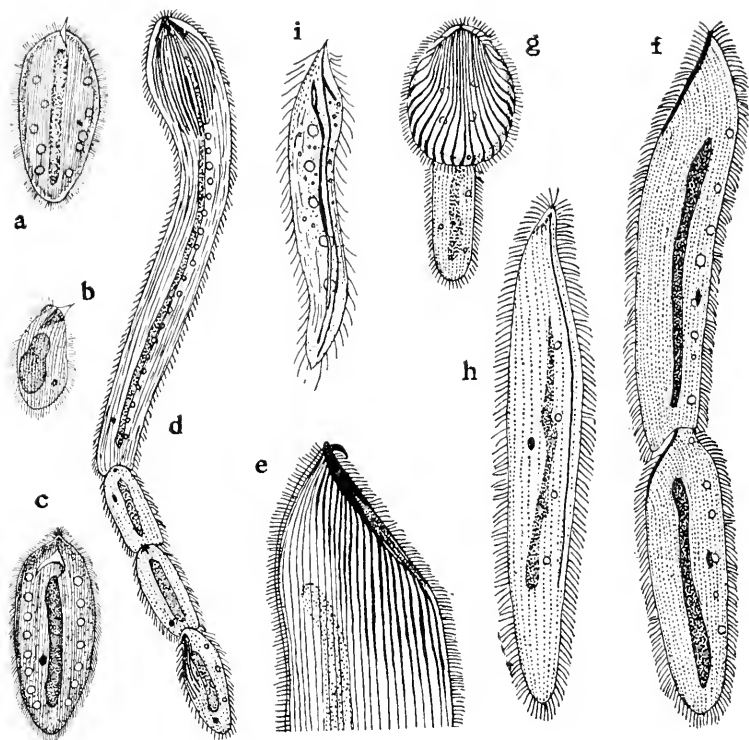


FIG. 228. a, *Maupasella nova*, $\times 280$ (Cépède); b, *Schultzellina mucronata*, $\times 670$ (Cépède); c, *Hoplitophrya lumbrici*, $\times 140$ (Cépède); d, e, *Radiophrya hoplites* (d, $\times 130$; e, anterior end in profile, $\times 300$) (Cheissin); f, *Protoradiophrya fissispiculata*, $\times 330$ (Cheissin); g, *Mrazeikiella intermedia*, $\times 210$ (Cheissin); h, *Mesnilella rostrata*, $\times 470$ (Cheissin); i, *M. clavata*, $\times 290$ (Penard).

Genus **Hoplitophrya** Stein. Ovoid to ellipsoid; chitinous protrusible attaching organella imbedded near anterior end; macronucleus an elongate band; contractile vacuoles in 2 longitudinal rows. Several species.

H. lumbrici (Dujardin) (Fig. 228, c). About 200μ long; in intestine of *Lumbricus terrestris*.

Genus **Radiophrya** Rossolimo. Elongate; attaching organella composed of arrowhead, tooth and ectoplasmic fibrils. Many species.

R. hoplites R. (Fig. 228, d, e). $100\text{--}1000\mu$ long; in intestine of *Lamprodrilus*, *Teleuscolex*, *Styloscolex* and other oligochaetes.

Genus **Protoradiophrya** Rossolimo. Elongate; near anterior end, a shallow depression, along which is found a spicule which may be split posteriorly. A few species.

P. fissispiculata Cheissin (Fig. 228, f). 180–350 μ long; in anterior portion of intestine of *Styloscolex* sp.

Genus **Mrazekiella** Kijenskij. Elongate; anterior portion broad with sucker-like depression, posterior region cylindrical; anterior end with attaching organella composed of arrowhead and skeletal ribs; macronucleus an elongate band; contractile vacuoles distributed. A few species.

M. intermedia Cheissin (Fig. 228, g). 180–260 μ long; in anterior portion of intestine of *Branchiura coccinea*.

Genus **Mesnilella** Cépède. Elongate; with one or more long spicules imbedded in endoplasm; contractile vacuoles in 1–2 rows. Numerous species.

M. rostrata Rossolimo (Fig. 228, h). 100–1200 μ long; in intestine of various oligochaetes (*Styloscolex*, *Teleuscolex*, *Lamprodrilus*, *Agriodrillus*, etc.).

M. clavata (Leidy) (Fig. 228, i). 100–200 μ long; in intestine of *Lumbricus variegatus*.

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CHAPTER 31

Order 1 **Holotricha** Stein (continued)

Suborder 2 **Gymnostomata** Bütschli

- Cytostome at or near anterior end.....Tribe 1 Prostomata
Cytostome not at or near anterior end
 Cytostome lateral, narrow or round.....
 Tribe 2 Pleurostomata (p. 517)
Cytostome ventral, in anterior half. Tribe 3 Hypostomata (p. 522)

Tribe 1 **Prostomata** Schewiakoff

Free-living

- Cytostomal region compressed; bearing trichites.....
 Family 1 Spathidiidae
 Cytostomal region not compressed
 Cytostome opens into anterior receptaculum; with lorica.....
 Family 2 Metacystidae (p. 499)
 Cytostome at tip of apical cone....Family 3 Didiniidae (p. 499)
 Cytostome otherwise
 Body covered with regularly arranged, perforated, ectoplasmic
 plates.....Family 4 Colepidae (p. 501)
 Body not covered with plates
 With radially arranged tentacles.....
 Family 5 Actinobolinidae (p. 503)
 Without tentacles.....Family 6 Holophryidae (p. 503)
Parasitic in mammalian gut.....Family 7 Butschliidae (p. 513)

Family 1 **Spathidiidae** Kahl

Genus **Spathidium** Dujardin. Flask- or sack-shaped; compressed; anterior region slightly narrowed into a neck, and truncate; ciliation uniform; cytostome occupies whole anterior end; contractile vacuole posterior; macronucleus elongate; several micronuclei; trichocysts around cytostome and scattered throughout; fresh or salt water. Numerous species.

S. spathula (Müller) (Figs. 21; 229, *a, b*). Up to 250 μ long; fresh water. Woodruff and Spencer (1922) made a careful study of the organism.

Genus **Paraspathidium** Noland. Form resembles that of *Spathidium*; but cytostome an elongate slit, bordered on one side by strong cilia and on the other by weaker ones and a shelf-like, non-undulatory membrane; 2 longer cilia on dorsal edge near anterior

tip; anterior 1/3 compressed; posterior 2/3 nearly cylindrical; 2 oval macronuclei, each with a micronucleus; cytoplasm filled with numerous refractile granules (metabolic reserves); about 70 rows of cilia; contractile vacuole terminal; salt water. One species.

P. trichostomum N. (Fig. 229, c-e). About 220μ long; macronuclei 44μ long each; salt water; Florida.

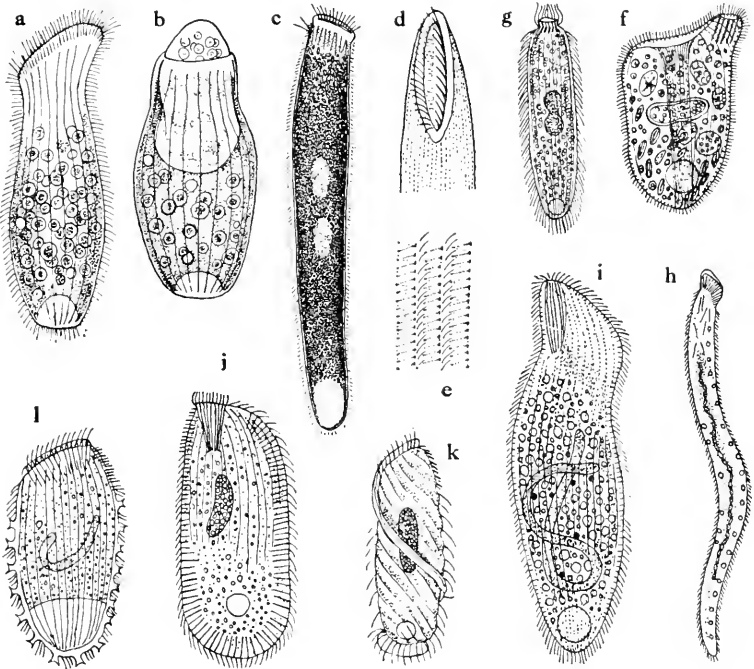


FIG. 229. a, b, *Spathidium spathula*, $\times 200$ (Woodruff and Spencer); c-e, *Paraspithidium trichostomum* (c, $\times 130$; d, cytostomal region, $\times 400$; e, part of pellicle, $\times 1000$) (Noland); f, *Spathidioides sulcata*, $\times 260$ (Brodsky); g, *Enchelydium fusidens*, $\times 240$ (Kahl); h, *Homalozoon vermiculare*, $\times 80$ (Stokes); i, *Cranotheridium taeniatum*, $\times 300$ (Schewiakoff); j, *Penardiella crassa*, $\times 210$ (Kahl); k, *Perispira strephosoma*, $\times 280$ (Kahl); l, *Legendrea bellerophon*, $\times 190$ (Penard).

Genus **Spathidioides** Brodsky (*Spathidiella* Kahl). Somewhat similar to *Spathidium*; but oral ridge highly flattened on ventral end, and most developed into wart-like swelling on dorsal end; this knob contains trichocysts; sapropelic.

S. sulcata B. (Fig. 229, f). $65-85\mu$ long; posterior end pointed,

highly flattened; anterior end elevated at one side where cytostome and cytopharynx with 10 rods are located.

Genus **Enchelydium** Kahl. Somewhat similar to *Spathidium*; but oral ridge forms a swollen ring with trichocysts, which is circular or elongated in cross-section; when swimming, the organisms appear as if cytostome is opened; with dorsal bristle; fresh water.

E. fusidens K. (Fig. 229, *g*). Cylindrical, contractile; cilia dense and rather long; macronucleus reniform, often appears as composed of 2 spherical parts; contractile vacuole terminal; oral ring with spindle-like trichocysts; food vacuoles not seen; extended body 110μ long; contracted 75μ ; sapropelic.

Genus **Homalozoon** Stokes. Elongate; cilia only on flattened right side; left side swollen or keeled; fresh water.

H. vermiculare (S.) (Fig. 229, *h*). Extended body $450\text{--}850\mu$ long; vermiform; numerous macronuclear parts in band form; contractile vacuoles about 30 or more in a row; standing pond water.

Genus **Cranotheridium** Schewiakoff. Spathidium-like organisms; anterior end obliquely truncate, near the extended side of which are located the cytostome, and cytopharynx surrounded by a group of trichites or trichocysts; fresh water.

C. taeniatum S. (Fig. 229, *i*). Anterior end flattened; with a group of trichites; macronucleus long band-form; with many micronuclei; contractile vacuole terminal; ciliation and striation close; colorless; movement slow; about 170μ long; fresh water.

Genus **Penardiella** Kahl. Ellipsoid, somewhat compressed; oral ridge slightly oblique; from this a girdle with trichocysts encircles body; fresh water.

P. crassa (Penard) (Fig. 229, *j*). Elongate ellipsoid, flattened; trichocysts in posterior portion of girdle are longer and those in the dorsal region are fewer in number and shorter; macronucleus sausage-form; contractile vacuole posterior, in front of the girdle; body 160μ by 50μ ; sapropelic.

Genus **Perispira** Stein. Ovoid or cylindrical; oral ridge turns down right-spirally to posterior end.

P. strephosoma Stokes (Fig. 229, *k*). Oval to cylindrical; about 85μ long; standing water, with sphagnum.

Genus **Legendrea** Fauré-Fremiet. Ellipsoid or ovoid; a peripheral zone with small tentacular processes bearing trichocysts.

L. bellerophon Penard (Fig. 229, *l*). 100–180 μ ; fresh water.

Genus **Teuthophrys** Chatton et Beauchamp. Body rounded posteriorly, anterior end with 3 radially equidistant, spirally curved arms (counter-clockwise when viewed from posterior end); the depressions between arms form furrows; cytostome apical, at the inner bases of arms; contractile vacuole terminal; ciliation uniform, except the inner surfaces of arms where longer cilia as well as trichocysts are present; with zoochlorellae; macronucleus rope-shaped and wound; micronucleus unobserved. One species.

T. trisula C. et B. (Fig. 230, *a*). 150–300 μ long; length: width 3:1–2:1; ponds in Pennsylvania and California (Wenrich).

Family 2 Metacystidae Kahl

Genus **Metacystis** Cohn. Oblong; definite; ciliation general, except posterior end; ciliary circle around cytostome; usually one caudal cilium; with a large posterior vesicle containing turbid fluid.

M. truncata C. (Fig. 230, *b*). Elongate, not much difference in body width at different levels; with about 12 furrow rings; body length up to 30 μ ; salt water.

Genus **Vasicola** Tatem (*Pelamphora* Lauterborn). Ovoid with caudal cilia; lorica flask-shape, highly ringed; cytostome at anterior end, its lip with 4 rows of long cilia; body surface with shorter cilia; macronucleus round, central, with a micronucleus; contractile vacuole near macronucleus and nearer body surface; fresh or salt water.

V. ciliata T. (*Pelamphora butschlii* Lauterborn) (Fig. 230, *c*). Body about 100 μ long; sapropelic in fresh water.

Genus **Pelatractus** Kahl. Somewhat similar to *Vasicola*; but without caudal cilia; with a large terminal vacuole; without lip of *Vasicola*; sapropelic.

P. (Vasicola) grandis (Penard) (Fig. 230, *d*). Free-swimming; elongated fusiform; numerous contractile vacuoles on side; body 125–220 μ long; sapropelic in fresh water.

Family 3 Didiniidae Poche

Genus **Didinium** Stein (*Monodinium* Fabre-Domergue). Barrel-shaped; one to several girdles of cilia (pectinellae); expansible cytostome at tip of cone-like elevation at anterior end, containing long trichites; macronucleus horseshoe-shaped; contractile vacu-

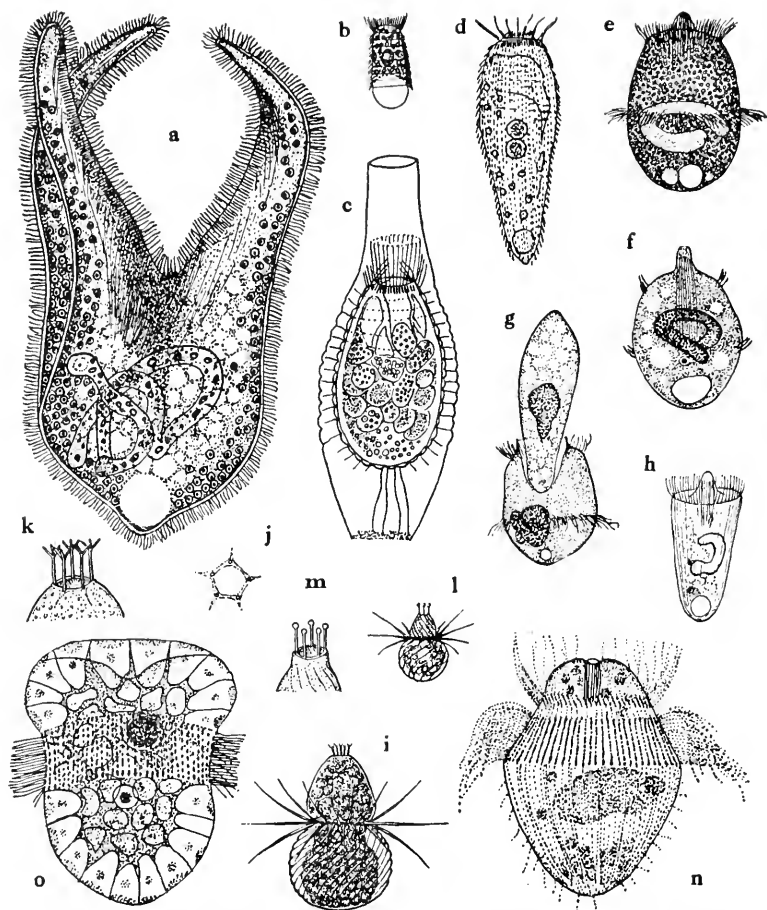


FIG. 230. a, *Tenthophrys trisula*, $\times 330$ (Wenrich); b, *Metacystis truncata*, $\times 270$ (Cohn); c, *Vasicola ciliata*, $\times 250$ (Kahl); d, *Pelatractus grandis*, $\times 170$ (Penard); e-g, *Didinium nasutum*, $\times 170$ (Kudo); h, *D. balbianii*, $\times 290$ (Bütschli); i-k, *Mesodinium pulex* (i, $\times 670$; j, oral view; k, oral tentacles, $\times 1330$) (Noland); l, m, *M. acarus* (l, $\times 670$; m, oral tentacles, $\times 1330$) (Noland); n, *Askenasia volvox*, $\times 530$ (Fauré-Fremiet); o, *Cyclotrichium meunieri*, $\times 780$ (Powers).

ole posterior; feeds on other ciliates, especially *Paramecium*; fresh or salt water. Several species.

D. nasutum (Müller) (Fig. 230, e-g). 80–200 μ long; endoplasm highly granulated; with 2 girdles of pectinelles; fresh water.

D. balbianii (Fabre-Domergue) (Fig. 230, h). 60–100 μ long; a single girdle of pectinelles near anterior end; fresh water.

Genus **Mesodinium** Stein. Ovoid; an equatorial furrow divides conical anterior and spherical posterior parts; in the furrow are inserted 2 (or 1) rings of strong cilia; one directed anteriorly and the other posteriorly; with tentacle-like retractile processes around the cytostome; fresh or salt water.

M. pulex (Claparède et Lachmann) (Fig. 230, *i-k*). Oral tentacles with trifurcate tips; body $20-31\mu$ long; salt water; Florida. Noland states that the freshwater forms are $21-38\mu$ long.

M. acarus Stein (Fig. 230, *l, m*). Oral tentacles with capitate tips; $10-16\mu$ long; salt water, Florida (Noland).

Genus **Askenasia** Blochmann. Resembles *Didinium*; ovoid; with 2 closely arranged rings of long cilia; anterior ring made up of some 60 pectinelles which are directed anteriorly; posterior ring composed of about the same number of membranellae or cirri, directed posteriorly and arranged parallel to body surface; fresh or salt water.

A. volvox (Claparède et Lachmann) (Fig. 230, *n*). Body oval, posterior end broadly rounded; anterior region conical; pectinelles about 13μ long; below the second ring of cirri are found long (40μ) bristles; a spherical macronucleus with a micronucleus; body about $50-60\mu$ long; fresh water.

Genus **Cyclotrichium** Meunier. Body spheroid to ellipsoid with a large non-ciliated oral field which is surrounded by a pectinellering, the remaining part naked or slightly ciliated; macronucleus sausage-form; cytopharynx not recognized; endoplasm highly vacuolated; in marine plankton.

C. meunieri Powers (Fig. 230, *o*). Anterior end broadly rounded; posterior region conical; cytostome obscure; oral funnel at anterior end in a depression; broad ciliated band at about middle; ectoplasm with concave chromatophore (haematochrome) plates on surface, below which numerous pyrenoids occur in vacuoles; endoplasm with numerous granules; $25-42\mu$ by $18-34\mu$; Powers (1932) found that the 'red water' in Frenchman Bay in Maine was caused by the swarming of this organism.

Family 4 **Colepidae** Claparède et Lachmann

Genus **Coleps** Nitzsch. Body-form constant, barrel-shaped; with regularly arranged ectoplasmic plates; cytostome at anterior end, surrounded by slightly longer cilia; often spinous projections at or near posterior end; 1 or more caudal cilia, often overlooked; fresh or salt water. Many species.

C. hirtus (Müller) (Fig. 231, a). 40–65 μ long; 15–20 rows of platelets; 3 posterior processes; fresh water.

C. elongatus Ehrenberg (Fig. 231, b). 40–55 μ long; slender; about 13 rows (Noland) or 14–17 rows (Kahl) of platelets; 3 posterior processes; fresh water.

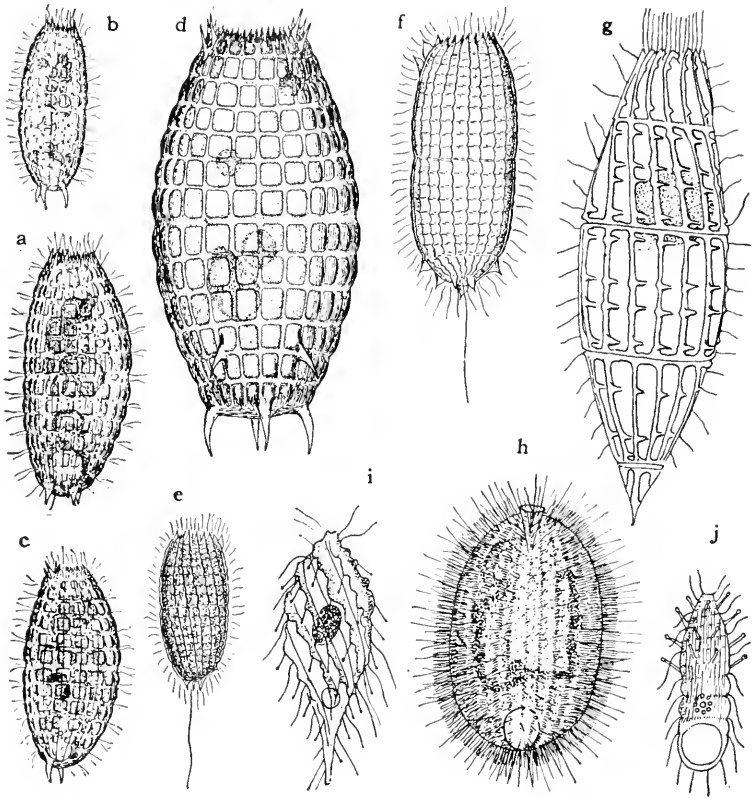


FIG. 231. a, *Coleps hirtus*, $\times 530$ (Noland); b, *C. elongatus*, $\times 530$ (Noland); c, *C. bicuspis*, $\times 530$ (Noland); d, *C. octospinus*, $\times 530$ (Noland); e, *C. spiralis*, $\times 400$ (Noland); f, *C. heteracanthus*, $\times 400$ (Noland); g, *Tiarina fuscus*, $\times 530$ (Fauré-Fremiet); h, *Actinobolina vorax*, $\times 300$ (Wenrich); i, *Dactyloclamys pisciformis*, $\times 330$ (Kahl); j, *Enchelyomorpha vermicularis*, $\times 670$ (Kahl).

C. bicuspis Noland (Fig. 231, c). About 55 μ long; 16 rows of platelets; 2 posterior processes; fresh water.

C. octospinus N. (Fig. 231, d). 80–110 μ long; 8 posterior spines;

about 24 rows of platelets; Geiman (1931) found this organism in an acid marsh pond and noted variation in number and location of accessory spines; fresh water.

C. spiralis N. (Fig. 231, *e*). About 23 longitudinal rows of platelets slightly spirally twisted; posterior spines drawn together; a long caudal cilium; about 50μ long; salt water; Florida.

C. heteracanthus N. (Fig. 231, *f*). Anterior processes only on one side; posterior spines; caudal cilium; about 90μ by 35μ ; salt water; Florida.

Genus **Tiarina** Bergh. Somewhat similar to *Coleps*, but posterior end tapering to a point; salt water.

T. fuscus (Claparède et Lachmann) (Fig. 231, *g*). $85\text{--}135\mu$ long.

Family 5 Actinobolinidae Kent

Genus **Actinobolina** Strand (*Actinobolus* Stein). Ovate or spherical; ciliation uniform; extensible tentacles among cilia; contractile vacuole terminal; macronucleus curved band; fresh water.

A. vorax (Wenrich) (Fig. 231, *h*). $100\text{--}200\mu$ long; elongate oval to spheroid; light yellowish brown in color; Wenrich (1929) found this ciliate in pond water and studied its behavior.

Genus **Dactylochlamys** Lauterborn. Body spindle-form, though variable; posterior end drawn out into tail; pellicle with 8–12 undulating spiral ridges on which tentacle-like processes and long cilia are alternately situated; these processes are retractile (Kahl) and similar in structure to those of Suctoria; cytostome has not been detected; possibly allied to Suctoria; fresh water. One species.

D. pisciformis L. (Fig. 231, *i*). Body $80\text{--}120\mu$ long.

Genus **Enchelyomorpha** Kahl. Conical, compressed; posterior end broadly rounded; anterior portion narrow; cilia on ring-furrows; anterior half with unretractile short tentacles; cytostome not noted; macronucleus with a central endosome surrounded by radiating spherules; contractile vacuole terminal, large.

E. vermicularis (Smith) (Fig. 231, *j*). Body $30\text{--}45\mu$; fresh and brackish water.

Family 6 Holophryidae Schouteden

Genus **Holophrya** Ehrenberg. Oval, globose or ellipsoidal;

ciliation uniform; sometimes longer cilia at anterior or posterior region; cytostome circular, simple, without any ciliary ring around it; cytopharynx with or without trichites or trichocysts; fresh or salt water. Numerous species.

H. simplex Schewiakoff (Fig. 233, *a*). Ellipsoidal; 18–20 ciliary rows; cilia uniformly long; cytostome small; cytopharynx without trichocysts or trichites; contractile vacuole and cytopyge posterior; macronucleus large, round; 34μ by 18μ ; fresh water.

Genus **Lagynophrya** Kahl. Resembles *Holophrya*; small elongate ovoid to short cylindrical; one side convex, the other more or less flattened; cytopharynx terminates anteriorly in a small cone-like process found in cross-section, which may or may not be distinct; stagnant fresh or salt water. Several species.

L. mutans K. (Fig. 233, *b*). Body plastic; oval to cylindrical; colorless; narrowly striated; oval cone hemispherical without any trichocysts; body about 90μ long, when contracted; about 65μ in diameter; among decaying leaves in fresh water.

Genus **Ichthyophthirius** Fouquet. Body oval; ciliation uniform; pellicle longitudinally striated; cytostome at anterior end, with a short cytopharynx with cilia; horseshoe-shaped macronucleus; micronucleus adhering to macronucleus, during encystment migrates toward surface of endoplasm; macronucleus undergoes reorganization by discarding small chromatin masses (Haas); multiplication by binary fission during actively motile stage or by multiple division in encysted condition, which produces 200 or more individuals (30 – 45μ long); conjugation also reported; parasitic in the integument of various freshwater fishes confined to aquarium or small pond; widely distributed.

I. multifiliis F. (Fig. 232). 300 – 800μ long; forms pustules in epidermis or gills; when heavily infected, the host fish suffer fatal effects; Pearson (1932) and Kudo (1934) reported an extensive ichthyophthirius-disease among fishes in large outdoor ponds in Indiana and Illinois.

Genus **Bursella** Schmidt. Oval; anterior end broadly and obliquely truncate where a large ciliated groove-like pit occurs; ridges of pit contractile; cilia short; macronucleus, spherical to ellipsoidal; several micronuclei; endoplasm reticulated; with symbiotic algae; ectoplasm with trichocysts; fresh water.

B. spumosa S. 240 – 560μ long; freshwater pond.

Genus **Spasmotoma** Kahl. Somewhat similar to *Holophorya*;

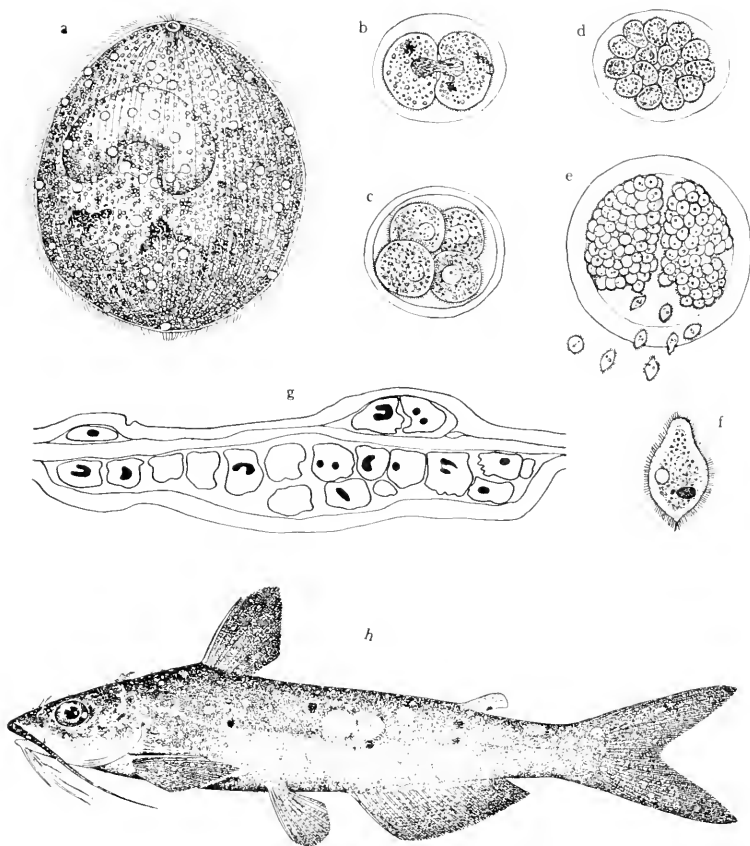


FIG. 232. *Ichthyophthirius multifiliis*. a, free-swimming individual, $\times 75$ (Bütschli); b-e, development within cyst; f, a young individual, $\times 400$ (Fouquet); g, section through a fin of infected carp showing numerous parasites, $\times 10$ (Kudo); h, a catfish, *Ameiurus albidus*, heavily infected by the ciliate (Stiles).

but without caudal cilia; cytostome with flaps which beat alternately; ciliation uniform.

S. viride K. (Fig. 233, c). Spherical or oval; always with green food vacuoles containing *Euglena* and allied flagellates; cytostome at anterior end; cytopharynx with trichocysts, which are extensible at the time when food is taken in; cilia on about 20 rows, near cytostome somewhat longer; macronucleus round; body $50-75\mu$ long; sapropelic.

Genus **Urotricha** Claparède et Lachmann (*Balanitozoon* Stokes). Body oval to ellipsoidal or conical; with 1 or more longer caudal cilia; ciliation uniform, except posterior region which may be without cilia; cytostome at or near anterior end, surrounded by ring of heavier cilia; contractile vacuole, posterior; macronucleus spherical; fresh water.

U. agilis (Stokes) (Fig. 233, *d*). Body small; about 15–20 μ long; swimming as well as leaping movement; standing fresh water with sphagnum.

U. farcta C. et L. (Fig. 233, *e*). Body 20–30 μ long; fresh water; Kahl considers *U. parvula* Penard and *Balanitozoon gyrans* Stokes are identical with this species.

Genus **Plagiocampa** Schewiakoff. Ovoid, spindle-form or cylindrical; slightly asymmetrical; cytostome at anterior end in a slit; right ridge thickened and lip-like, with about 8 long cilia; with or without long caudal cilium; fresh or salt water. Several species.

P. marina Kahl (Fig. 233, *f, g*). Cylindrical; oval macronucleus central; contractile vacuole terminal; a caudal cilium; 55–90 μ long; salt water; Florida (Noland).

Genus **Chilophrya** Kahl. Ovoid or ellipsoid; cytostome at anterior end, surrounded by protrusible rods; on one side there is a lip-like ectoplasmic projection; fresh or salt water.

C. (Prorodon) utahensis (Pack) (Fig. 233, *h*). Body ellipsoid, somewhat asymmetrical; comparatively small number of furrows; ciliation uniform; a finger-like process in front of cytostome; macronucleus small, central; contractile vacuole terminal; endoplasm with zoochlorellae; encystment common; cysts highly sensitive to light; 50 μ long; Great Salt Lake; Utah (Pack).

C. (Urotricha) labiata (Edmondson) (Fig. 233, *i*). Body ovoid; a lip-like process in front of cytostome; macronucleus oblong, central; contractile vacuole terminal; 30 μ long; fresh water.

Genus **Platyophrya** Kahl. Compressed; flask-like or elongate ovoid; asymmetrical; dorsal surface convex, ventral surface flat or partly concave; spiral striation; position and direction of cytostome variable; macronucleus round; contractile vacuole terminal; fresh water.

P. lata K. (Fig. 233, *j*). Highly compressed; colorless; many striae; on left edge of cytostome 5–6 cirrus-like projections and on right edge many short bristles; 105 μ long; fresh water with sphagnum.

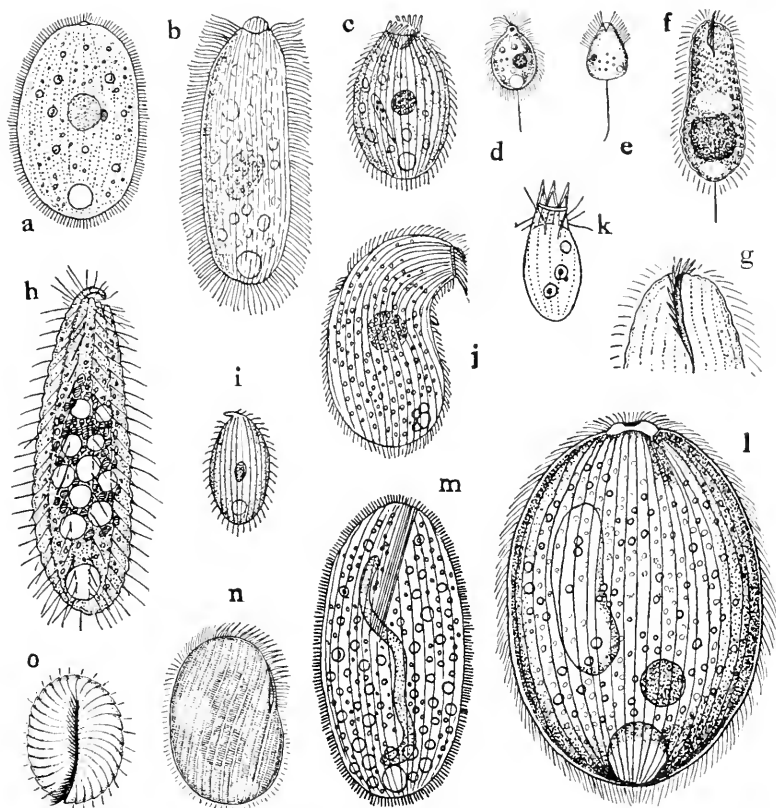


FIG. 233. a, *Holophrya simplex*, $\times 800$ (Roux); b, *Lagynophrya mutans*, $\times 380$ (Kahl); c, *Spasmostoma viride*, $\times 330$ (Kahl); d, *Urotricha agilis*, $\times 530$ (Stokes); e, *U. farcta*, $\times 470$ (Lieberkühn); f, g, *Plagiocampa marina* (f, $\times 400$; g, anterior end, $\times 670$) (Noland); h, *Chilophrya utahensis*, $\times 840$ (Pack); i, *C. labiata*, $\times 500$ (Edmondson); j, *Platyophrya lata*, $\times 280$ (Kahl); k, *Stephanopogon colpoda*, non-ciliated side, $\times 500$ (Kahl); l, *Prorodon discolor*, $\times 330$ (Bütschli); m, *Pseudoprorodon farctus*, $\times 270$ (Roux); n, o, *Placus socialis* (o, anterior end view), $\times 530$ (Noland).

Genus **Stephanopogon** Entz. Somewhat resembles *Platyophrya*; compressed; cytostome at anterior extremity which is drawn out; cytostome surrounded by lobed membranous structures; salt water.

S. colpoda E. (Fig. 233, k). Longitudinal striae on 'neck' 4-8 in number; 2 contractile vacuoles; $50-70\mu$ long; creeping movement; salt water among algae.

Genus **Prorodon** Ehrenberg (*Rhagadostoma* Kahl). Ovoid to cylindrical; ciliation uniform, with sometimes longer caudal cilia; oral basket made up of double trichites which end deep in ectoplasm, oval in cross-section; contractile vacuole terminal; macronucleus massive, spherical or oval; fresh or salt water. Numerous species.

P. discolor (E.) (Fig. 233, *l*). Ovoidal; 45–55 ciliary rows; macronucleus ellipsoid; micronucleus hemispherical; contractile vacuole terminal; 100–130 μ long; fresh water; Kahl (1930) states that it occurs also in brackish water containing 2.5 per cent salt; sapropelic form in salt water is said to possess often long caudal cilia.

P. griseus Claparède et Lachmann. Oblong; 165–200 μ long; fresh water.

Genus **Pseudoprorodon** Blochmann. Similar to *Prorodon*; usually flattened; one side convex, the other concave; ectoplasm conspicuously alveolated; trichocysts grouped; 1 or more contractile vacuoles posterior-lateral or distributed, with many pores; macronucleus elongate; cytopharynx with trichites; fresh or salt water.

P. faretus (Claparède et Lachmann) (Fig. 233, *m*). Ellipsoid; cytostome surrounded by long trichocysts; contractile vacuole posterior, with secondary vacuoles; macronucleus elongate; body 150–200 μ long; fresh water.

Genus **Placus** Cohn (*Spathidiopsis* Fabre-Domergue; *Thoracophrya* Kahl). Body small; ellipsoid or ovoid; somewhat compressed; pellicle with conspicuous spiral furrows; cytostome a narrow slit at anterior extremity; with strong cilia on right margin of slit; cytopyge a long narrow slit with cilia on both sides; macronucleus ellipsoid to sausage-form; contractile vacuole posterior; salt, brackish or fresh water.

P. socialis (Fabre-Domergue) (Fig. 233, *n, o*). 40–50 μ by 28–32 μ , about 22 μ thick; salt water; Florida.

Genus **Lacrymaria** Ehrenberg. Polymorphic; cylindrical, spindle- or flask-shaped; with a long contractile proboscis; cytostome round; ciliary rows meridional or spiral to right; near cytostome a ring-like constriction with a circle of longer cilia; cytopharynx usually distinct; contractile vacuole terminal; fresh or salt water. Numerous species.

L. olor (Müller) (Fig. 234, *a*). Elongate; highly contractile;

2 macronuclei; 2 contractile vacuoles; extended forms 400–500 μ up to 1.2 mm. long; when dividing, long neck is formed sidewise so that it appears as oblique division (Penard); fresh and salt water.

L. lagenula Claparède et Lachmann (Fig. 234, *b*). Body flask-shape; neck highly extensible; striation distinct, spiral when contracted; macronucleus short sausage-like or horseshoe-shape; endoplasm granulated; body 70 μ long, up to 150 μ (Kahl); salt water.

L. coronata C. et L. (Fig. 234, *c*). Large; neck extensible; body form variable, but usually with bluntly pointed posterior end; endoplasm appears dark; striae spiral; 85–100 μ long; salt and brackish water.

Genus **Enchelys** Hill. Flask-shape; anterior end obliquely truncate; cytostome slit-like, rarely round; fresh or salt water. Several species.

E. curvilata (Smith) (Fig. 234, *d*). Elongate ovoid; posterior end rounded; longitudinal striation; macronucleus band-form; contractile vacuole terminal; endoplasm yellowish, granulated; about 150 μ long; fresh water among algae.

Genus **Crobylura** André. Body when extended spindle-form, with truncate ends; when contracted, thimble-form; cilia short and thick; several long caudal cilia; slit-like cytostome at anterior end; no apparent cytopharynx; macronucleus irregularly rounded, hard to stain; micronucleus not observed; contractile vacuole latero-posterior; fresh water. One species.

C. pelagica A. (Fig. 234, *e*). Body 65–95 μ long; in freshwater plankton.

Genus **Microregma** Kahl. Small, ovoid; dorsal side convex; ventral side flat; with a small slit-like cytostome near anterior end; with or without caudal bristle; fresh or salt water.

M. (Enchelys) auduboni (Smith) (Fig. 234, *f*). Body plastic; coarsely ciliated; caudal bristle thin; cytostome at anterior end, surrounded by longer cilia; cytopharynx small with trichocysts; round macronucleus central; contractile vacuole near posterior end; 40–55 μ ; fresh water.

Genus **Chaenea** Quennerstedt. Elongate; anterior end drawn out into a narrow truncated 'head'; but without any ring furrow; 'head' spirally or longitudinally furrowed; often with longer cilia directed anteriorly; cytostome terminal, not lateral; cytopharynx

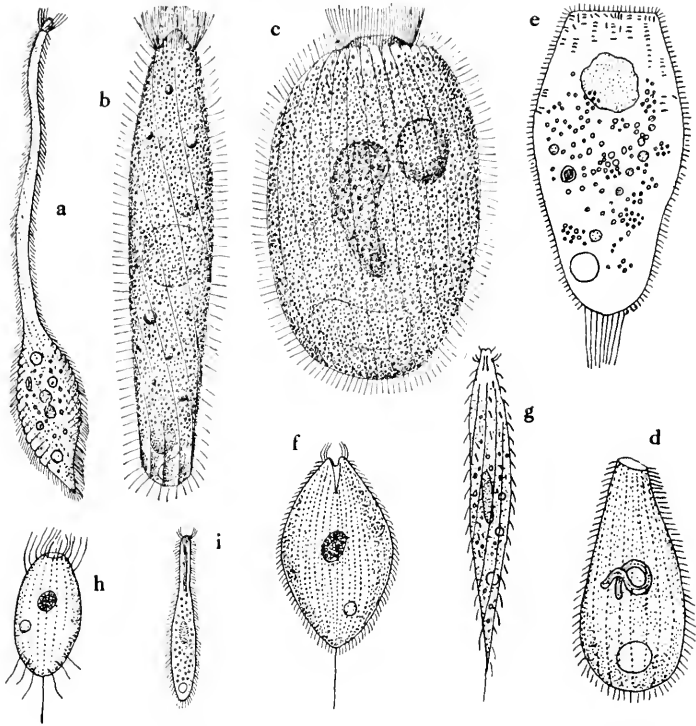


FIG. 234. a, *Lacrymaria olor*, $\times 170$ (Roux); b, *L. lagenula*, $\times 400$ (Calkins); c, *L. coronata*, $\times 530$ (Calkins); d, *Enchelys curvilata*, $\times 200$ (Smith); e, *Crobylura pelagica*, $\times 500$ (André); f, *Microregma auduboni* $\times 500$ (Smith); g, *Chaenca limicola*, $\times 310$ (Penard); h, *Pithothorax ovatus*, $\times 550$ (Kahl); i, *Trachelophyllum clavatum*, $\times 100$ (Stokes).

with trichocysts; body striation meridional, or slightly right spiral; macronucleus often distributed; fresh or salt water.

C. limicola Lauterborn (Fig. 234, g). Anterior half of body broad; posterior end drawn out into a point; contractile; cytopharynx with trichocysts; many trichocysts in endoplasm; contractile vacuoles in chain form; $130\text{--}150\mu$ long; stagnant fresh water.

Genus **Pithothorax** Kahl. Slender, barrel-shaped; with firm pellicle; a fairly long caudal bristle; contractile vacuole in posterior half; ciliation coarse and not over entire body surface; resembles somewhat *Coleps*; fresh water.

P. ovatus K. (Fig. 234, h). Caudal bristle breaks off easily; body 30μ long; fresh water among decaying vegetation.

Genus **Rhopalophrya** Kahl. Cylindrical; furrows widely separated; slightly asymmetrical; curved ventrally; dorsal surface convex; ventral surface flat or slightly concave; anterior end with 'neck'; 2 spherical macronuclei; fresh or salt water; sapropelic.

R. salina Kirby (Fig. 235, *a*). Cylindrical, tapering gradually to a truncated anterior end, slightly curved ventrally; cilia ($6-10\mu$ long) sparsely distributed; 2 macronuclei, spherical; $29-55\mu$ long; $16-21\mu$ in diameter; in concentrated brine (salts 34.8 per cent; pH 9.48) from Searles Lake; California.

Genus **Enchelyodon** Claparède et Lachmann. Elongated; cylindrical, ovoid or flask-shaped; some with head-like prolongation; cytopharynx with trichites; cilia long at anterior end; fresh or salt water. Several species.

E. farctus C. et L. (Fig. 21, *b*). Ellipsoid; ectoplasm thick, yellowish, with trichocyst layer; cilia dense and short; oral cone flat; cytopharynx with about 80μ long trichites; macronucleus long; contractile vacuole terminal; $180-400\mu$ long; fresh water among decaying vegetation.

E. californicus Kahl. $120-130\mu$ long; elongate ovoid to nearly cylindrical; not distinctly flattened; macronucleus horseshoe-like, with a large micronucleus; in mosses; California.

Genus **Trachelophyllum** Claparède et Lachmann. Elongate; flattened; flexible, ribbon-like; anterior end neck-like and tip truncate, cytopharynx narrow, round in cross-section, with trichocysts; ciliary rows widely apart; 2 macronuclei, each with a micronucleus; contractile vacuole terminal; fresh or salt water. Several species.

T. clavatum Stokes (Fig. 234, *i*). About 180μ long; fresh water.

Genus **Ileonema** Stokes (*Monomastix* Roux). Body flattened; flask-shaped; somewhat similar to *Trachelophyllum*, but differs by the fact that there is a remarkable flagellum-like process extending from anterior end; cytopharynx with trichocysts; fresh water.

I. dispar S. (Fig. 235, *b*). Highly contractile; anterior flagellum half body length, whose basal portion spirally furrowed; cytostome at base of the flagellum; cytopharynx spindle-form with trichites; 2 contractile vacuoles and cytopyge posterior; ovoid macronucleus; movement slow creeping; about 120μ long; fresh water among algae.

I. ciliata (Roux) (Fig. 235, *c*). 75μ by 14μ ; fresh water.

Genus **Trachelocerca** Ehrenberg. Elongate, vermiform or

flask-shaped; more or less extensible, with drawn-out anterior end; without ring-furrow which marks 'head' of *Lacrymaria*, and when contracted pellicular striae not spiral and no neck as is the case with *Chaenea*; salt water. Many species.

T. phoenicopterus Cohn (Fig. 235, d, e). Elongate; extensible and contractile; neck and tail distinct when contracted; cyto-

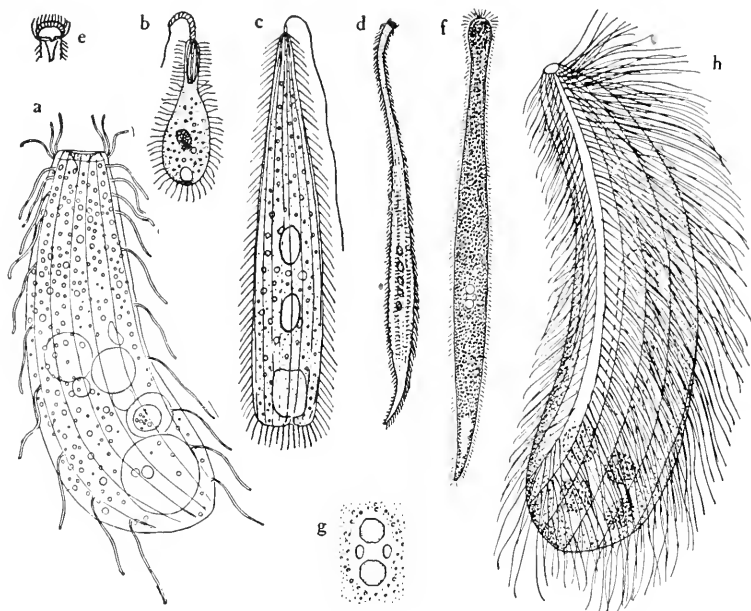


FIG. 235. a, *Rhopalophrya salina*, $\times 870$ (Kirby); b, *Ileonema dispar*, $\times 160$ (Stokes); c, *I. citiata*, $\times 670$ (Roux); d, e, *Trachelocerca phoenicopterus* (d, $\times 100$; e, anterior end, $\times 220$) (Kahl); f, g, *T. subviridis* (f, $\times 130$; g, nucleus, $\times 400$) (Noland); h, *Parachaenia myae*, $\times 670$ (Kofoid and Bush).

stome at anterior end, surrounded by a ridge containing indistinctly visible short trichocysts; cytopharynx with trichocysts; macronuclei made up of 4 radially arranged endosomes suspended in nucleoplasm (Gruber, Kahl); micronucleus difficult to make out; contractile vacuoles apparently in chain, rarely seen; salt water; Woods Hole (Calkins).

T. subviridis Sauerbrey (Fig. 235, f, g). Highly extensible and contractile; nucleus contains peculiar crystal-like bodies; size

variable; when extended $320\text{--}480\mu$ long; salt water. Noland observed the organism in a salt spring in Florida.

Genus **Parachaenia** Kofoid et Bush. Small; compressed; ventral surface slightly concave; dorsal surface greatly convex; cilia long, differentiated into 2 areas, a ventral area consisting of close-set rows and a dorso-lateral area consisting of 7 rows; cytostome circular or slightly oval, at anterior tip; cytopharynx long, narrow; without contractile vacuole. One species.

P. myae K. et B. (Fig. 235, *h*). $40\text{--}100\mu$ long; 7 rows of long cilia on dorso-lateral surfaces, 8 rows of shorter cilia on ventral surface; cytopharynx half body length; in pericardial cavity and siphon of *Mya arenaria*; San Francisco Bay.

Family 7 Butschliidae Poche

This family includes forms which are intestinal parasites of mammals; circular cytostome at anterior end, cytoproct usually located at posterior end; ciliation uniform or in a few zones; with refractile concretion vacuole or vesicle (Fig. 30, *d*) in anterior portion; one or more contractile vacuoles.

Genus **Butschlia** Schuberg. Ovoid, anterior end truncate, posterior end rounded; cytostome at anterior end, surrounded by long cilia; thick ectoplasm at anterior end; macronucleus spherical, micronucleus(?); concretion vacuole; ciliation uniform; in stomach of cattle.

B. parva S. (Fig. 236, *a*). $30\text{--}50\mu$ by $20\text{--}30\mu$.

Genus **Blepharoprosthium** Bundle. Pyriform, anterior half contractile, ciliated; caudal cilia; macronucleus reniform; in caecum and colon of horse.

B. pireum B. (Fig. 236, *b*). $54\text{--}86\mu$ by $34\text{--}52\mu$.

Genus **Didesmis** Fiorentini. Anterior end neck-like, with large cytostome; anterior and posterior ends ciliated; macronucleus ellipsoid; in caecum and colon of horse.

D. quadrata F. (Fig. 236, *c*). $50\text{--}90\mu$ by $33\text{--}68\mu$; with a deep dorsal groove.

Genus **Blepharosphaera** Bundle. Spherical or ellipsoidal; ciliation uniform except posterior region; caudal cilia; in caecum and colon of horse.

B. intestinalis B. (Fig. 236, *d*). $38\text{--}74\mu$ in diameter.

Genus **Blepharoconus** Gassovsky. Oval; small cytostome; cilia on anterior $1/3\text{--}1/2$; caudal cilia; macronucleus ovoid; 3 contractile vacuoles; cytopharynx with rods; in colon of horse.

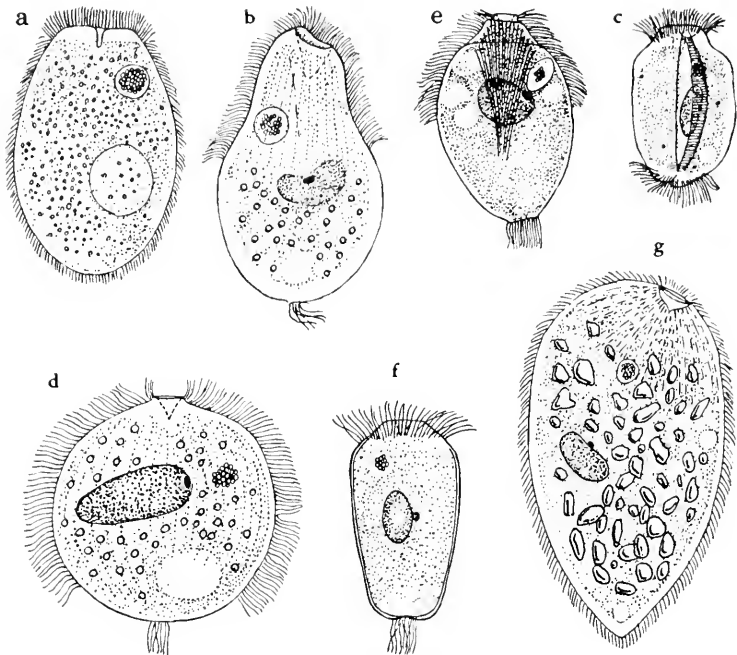


FIG. 236. a, *Butschlia parva*, $\times 670$ (Schuberg); b, *Blepharoprosthium pireum*, $\times 470$ (Hsiung); c, *Didesmis quadrata*, $\times 270$ (Hsiung); d, *Blepharosphaera intestinalis*, $\times 600$ (Hsiung); e, *Blepharoconus cervicalis*, $\times 360$ (Hsiung); f, *Bundleia postciliata*, $\times 530$ (Hsiung); g, *Blepharozoum zonatum*, $\times 200$ (Gassovsky).

B. cervicalis Hsiung (Fig. 236, e). $56\text{--}83\mu$ by $48\text{--}70\mu$; Iowa.

Genus **Bundleia** da Cunha et Muniz. Ellipsoid; cytostome small; cilia at anterior and posterior ends, posterior cilia much less numerous; in caecum and colon of horse.

B. postciliata (Bundle) (Fig. 236, f). $30\text{--}56\mu$ by $17\text{--}32\mu$.

Genus **Polymorpha** Dogiel. Flask-shaped; ciliation on anterior region, a few caudal cilia; macronucleus disc-shaped; contractile vacuole terminal; in caecum and colon of horse.

P. ampulla D. (Fig. 237, a). $22\text{--}36\mu$ by $13\text{--}21\mu$.

Genus **Holophryoides** Gassovsky. Oval, with comparatively large cytostome at anterior end; ciliation uniform; macronucleus small, ellipsoid; contractile vacuole subterminal; in colon and caecum of horse.

H. ovalis (Fiorentini) (Fig. 237, b). $95\text{--}140\mu$ by $65\text{--}90\mu$.

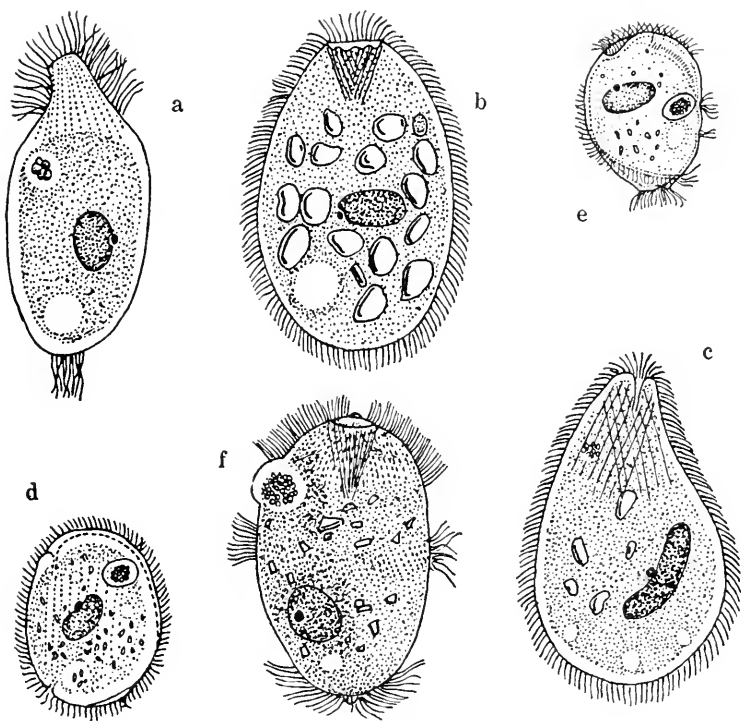


FIG. 237. a, *Polymorpha ampulla*, $\times 1170$ (Hsiung); b, *Holophryoides ovalis*, $\times 410$ (Gassovsky); c, *Prorodonopsis coli*, $\times 700$ (Gassovsky); d, *Paraisotrichopsis composita*, $\times 450$ (Hsiung); e, *Sulcoarcus pellucidulus*, $\times 410$ (Hsiung); f, *Alloiozona trizona*, $\times 450$ (Hsiung).

Genus **Blepharozoum** Gassovsky. Ellipsoid, with attenuated posterior end; ciliation uniform; cytostome near anterior tip; 2 contractile vacuoles; macronucleus small, reniform; in caecum of horse.

B. zonatum G. (Fig. 236, g). $230\text{--}245\mu$ by $115\text{--}122\mu$.

Genus **Prorodonopsis** Gassovsky. Pyriform; ciliation uniform; 3 contractile vacuoles; macronucleus sausage-shaped; in colon of horse.

P. coli G. (Fig. 237, c). $55\text{--}67\mu$ by $38\text{--}45\mu$.

Genus **Paraisotrichopsis** Gassovsky. Body uniformly ciliated; spiral groove from anterior to posterior end; in caecum of horse.

P. composita G. (Fig. 237, d). $43\text{--}56\mu$ by $31\text{--}40\mu$.

Genus **Sulcoarcus** Hsiung. Ovoid, compressed; a short spiral

groove at anterior end; cytostome at ventral end of the groove; cypopyge terminal; concretion vacuole mid-ventral, contractile vacuole posterior to it; cilia on groove, posterior end and mid-ventral region.

S. pellucidulus H. (Fig. 237, *e*). 33–56 μ by 30–40 μ ; in faeces of mule.

Genus **Alloiozona** Hsiung. Cilia in 3 (anterior, equatorial and posterior) zones; in caecum and colon of horse.

A. trizona H. (Fig. 237, *f*). 50–90 μ by 30–60 μ .

Genus **Ampullacula** Hsiung. Flask-shaped; posterior half bearing fine, short cilia; neck with longer cilia, in caecum of horse.

A. ampulla (Fiorentini). About 110 μ by 40 μ .

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CHAPTER 32

Order 1 **Holotricha** Stein (continued)

Suborder 2 **Gymnostomata** Bütschli (continued)

Tribe 2 **Pleurostomata** Schewiakoff

Cytostome on convex ventral surface

Cytostome a long slit.....Family 1 **Amphileptidae**

Cytostome round, at base of trichocyst-bearing neck

.....Family 2 **Tracheliidae** (p. 519)

Cytostome on concave ventral side....Family 3 **Loxodidae** (p. 521)

Family 1 **Amphileptidae** Schouteden

Genus **Amphileptus** Ehrenberg. Flask-shaped; somewhat compressed; ciliation uniform and complete; slit-like cytostome not reaching the middle of body; without trichocyst-borders; many contractile vacuoles; 2 or more macronuclei; fresh or salt water.

A. claparedei Stein (*A. meleagris* Claparède et Lachmann) (Fig. 238, *a*). Slightly flattened; broadly flask-shaped; with round posterior and neck-like anterior end; cytostome about $\frac{2}{5}$ from ventral margin; trichocysts indistinct; dorsal ciliary rows also not distinct; contractile vacuoles irregularly distributed; 120–150 μ long; fresh and salt water, on stalks of *Zoothamnium*, *Carchesium*, *Epistylis*, etc.

A. branchiarum Wenrich (Fig. 238, *b*). On integument and gills of frog tadpoles; swimming individuals killed with iodine, 100–135 μ by 40–60 μ .

Genus **Lionotus** Wrzeniowski (*Hemiophrys* W.). Flask-shape; elongate, flattened; anterior region neck-like; cilia only on right side; without trichocyst-borders; cytostome with trichocysts; 1 (terminal) or many (in 1–2 rows) contractile vacuoles; 2 macronuclei; 1 micronucleus; fresh or salt water.

L. fasciola (Ehrenberg) (Fig. 238, *c*). Elongate flask in form; hyaline; with flattened neck and tail, both of which are moderately contractile; posterior end bluntly rounded; without trichocysts; neck stout, bent toward the dorsal side; cytostome a long slit; contractile vacuole posterior; 2 spherical macronuclei between which a micronucleus is located; 100 μ long; fresh water and probably also in salt water.

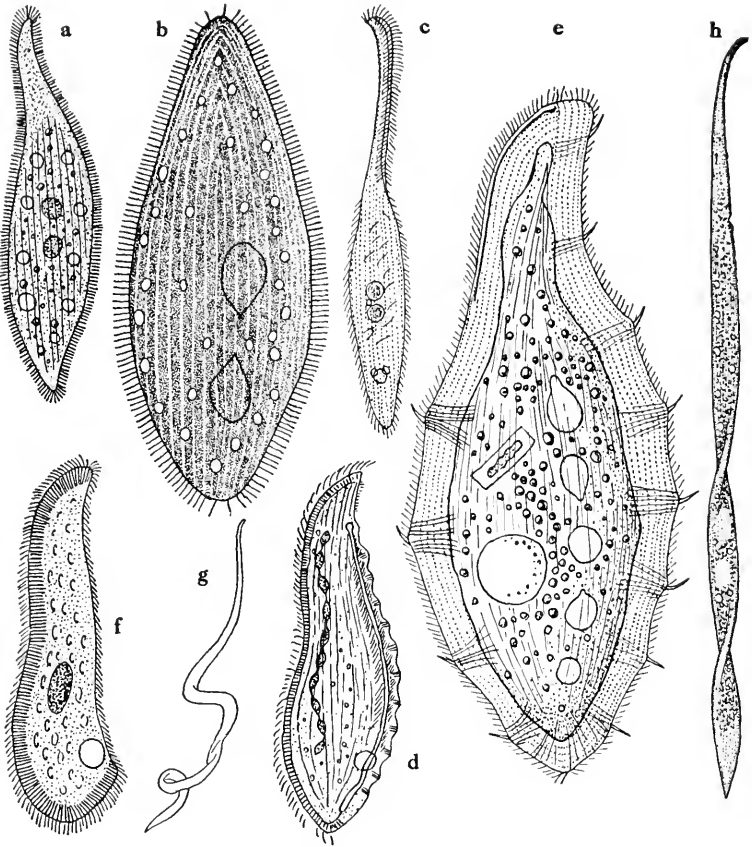


FIG. 238. a, *Amphileptus claparedei*, $\times 370$ (Roux); b, *A. branchiarum*, flattened, $\times 490$ (Wenrich); c, *Lionotus fasciola*, $\times 540$ (Kahl); d, *Loxophyllum meleagris*, $\times 120$ (Penard); e, *L. setigerum*, $\times 570$ (Sauerbrey); f, *Bryophyllum vorax*, $\times 360$ (Stokes); g, h, *Kentrophoros fasciolatum* (g, $\times 50$; h, $\times 110$) (Noland).

Genus **Loxophyllum** Dujardin (*Opisthodon* Stein). Generally similar to *Lionotus* in appearance; but ventral side with a hyaline border, reaching posterior end and bearing trichocysts; dorsal side with either similar trichocyst-border or with trichocyst-warts; macronucleus a single mass or in many parts; contractile vacuoles, 1 to many; fresh or salt water. Many species.

L. meleagris (D.) (Fig. 238, d). Form and size highly variable; flask-shape to broad leaf-like; broad ventral seam with tricho-

cysts and often undulating; dorsal seam narrow and near its edge, groups of trichocysts in wart-like protuberances; macronucleus divided into small ellipsoidal parts; micronuclei, of the same number (Penard); contractile vacuole terminal, with a long canal; 300–400 μ long, up to 700 μ (Penard); feeds mainly on rotifers; fresh water.

L. setigerum Quennerstedt (Fig. 238, *e*). 100–350 μ long; average 150 μ by 60 μ ; form variable; 1–4 macronuclei; several contractile vacuoles in a row; salt and brackish water.

Genus **Bryophyllum** Kahl. Similar to *Loxophyllum*; but uniformly ciliated on both broad surfaces; ventral ridge with closely arranged trichocysts, extends to the posterior extremity and ends there or may continue on the opposite side for some distance; macronucleus ovoid to coiled bandform; in mosses.

B. (Loxophyllum) vorax (Stokes) (Fig. 238, *f*). Elongate; trichocyst-bearing ventral ridge turns up a little on dorsal side; contractile vacuole posterior; macronucleus oval; 130 μ long; in fresh water among sphagnum and mosses.

Genus **Kentrophoros** Sauerbrey. Extremely elongate, nematode-like; anterior end greatly attenuated; posterior end pointed; body surface longitudinally striated; ciliation uniform; 1–3 macronuclei; numerous contractile vacuoles in 2 rows; cytostome not observed.

K. fasciolatum S. (Fig. 238, *g, h*). About 270 μ by 38 μ . Noland (1937) observed 2 specimens in sediment taken from sandy bottom in Florida; contracted 650 μ long; extended 1 mm. long.

Family 2 Tracheliidae Kent

Genus **Trachelius** Schrank. Oval to spherical; anterior end drawn out into a relatively short finger-like process or a snout; posterior end rounded; round cytostome at base of neck; cytopharynx with trichites; contractile vacuoles many; macronucleus simple or band-form; fresh water.

T. ovum Ehrenberg (Fig. 239, *a*). Spheroidal to ellipsoid; right side flattened and with a longitudinal groove; left side convex; proboscis about 1/4–1/2 the body length; cilia short and closely set; numerous contractile vacuoles; macronucleus short sausage-form, often divided into spherules; endoplasm penetrated by branching cytoplasmic skeins or bands and often with numerous small brown excretion granules; 200–400 μ long; fresh water.

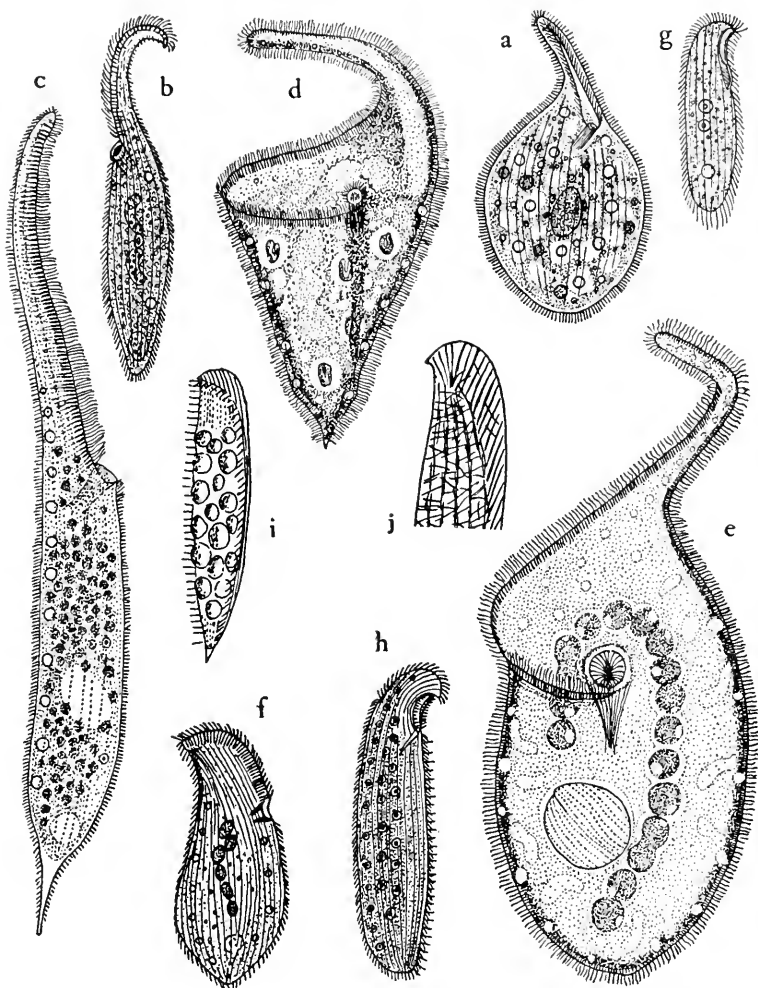


FIG. 239. a, *Trachelinus ovum*, $\times 130$ (Roux); b, *Dileptus americanus*, $\times 250$ (Kahl); c, *D. anser*, $\times 310$ (Hayes); d, *Paradileptus conicus*, $\times 340$ (Wenrich); e, *P. robustus*, $\times 340$ (Wenrich); f, *Branchioecetes gammari*, $\times 200$ (Penard); g, *Loxodes vorax*, $\times 190$ (Stokes); h, *L. magnus*, $\times 80$ (Kahl); i, j, *Remanella rugosa* (i, dorsal side, $\times 130$; j, anterior part showing the endoskeleton) (Kahl).

Genus **Dileptus** Dujardin. Elongate; snout or neck-like prolongation conspicuous; somewhat bent dorsally; along convex ventral side of neck many rows of trichocysts; a row of strong

cilia; dorsal surface with 3 rows of short bristles; cytostome surrounded by a ring; cytopharynx with long trichocysts; posterior end drawn out into a tail; contractile vacuoles, 2 or more; body ciliation uniform; macronucleus bandform, moniliform or divided into numerous independent bodies; fresh or salt water. Many species.

D. americanus Kahl (Fig. 239, *b*). Proboscis bent dorsally sickle-like; macronucleus made up of 2 sausage-shaped or often horseshoe-shaped parts; 2 contractile vacuoles on dorsal side; 200 μ long; in mosses.

D. anser (Müller) (Figs. 22, *c, d*; 239, *c*). Proboscis slightly flattened; macronucleus divided into numerous bodies; contractile vacuoles in a row on dorsal side with 2–3 contractile vacuoles in proboscis; 250–400 μ , sometimes up to 600 μ long; fresh water.

Genus **Paradileptus** Wenrich (*Tentaculifera* Sokoloff). Body broader at the level of cytostome; with a wide peristomal field which bears the cytostome and is surrounded for 2/3–3/4 its circumference by a raised rim which is continuous anteriorly with the spirally wound proboscis; trichocyst-zone traversing rim and anterior edge of proboscis; contractile vacuoles small, numerous, distributed; macronucleus segmented; fresh water.

P. conicus W. (Fig. 239, *d*). 100–200 μ by 50–100 μ .

P. robustus W. (Fig. 239, *e*). 180–450 μ long.

Genus **Branchioecetes** Kahl. Preoral part somewhat like that of *Amphileptus*, and bent dorsally; ventral side of neck with 2 rows of trichocysts; cytostome at posterior end of neck; cytopharynx with trichocysts; ectocommensals on Asellus or Gammarus.

B. gammari (Penard) (Fig. 239, *f*). 130–200 μ long; on Gammarus.

Family 3 Loxodidae Roux

Genus **Loxodes** Ehrenberg. Lancet-like; strongly compressed; anterior end curved ventrally, and usually pointed; right side slightly convex; uniform ciliation on about 12 longitudinal rows; ectoplasm appears brownish, because of closely arranged brownish protrichocysts; endoplasm reticulated; 2 or more vesicular macronuclei; 1 or more micronuclei; 5–25 Müller's vesicles (p. 77; Fig. 30, *a, b*) in dorsal region; fresh water.

L. vorax Stokes (Fig. 239, *g*). 125–140 μ long; yellowish brown, a row of slightly longer cilia; sapropelic in standing fresh water.

L. magnus S. (Fig. 239, *h*). Extended about 700μ long; dark brown; 12–20 or more Müller's vesicles in a row along dorsal border; standing pond water.

Genus **Remanella** Kahl. Similar to *Loxodes* in general appearance; but with endoskeleton consisting of 12– 20μ long spindle-form needles lying below ciliated broad surface in 3–5 longitudinal strings connected with fibrils; Müller's vesicles (Fig. 30, *c*) in some, said to be different from those of *Loxodes* (Kahl); sandy shore of sea.

R. rugosa K. (Fig. 239, *i, j*). 200– 300μ long.

Tribe 3 **Hypostomata** Schewiakoff

Without furrow; free-living; conspicuous oral or pharyngeal basket

Ciliation complete; dorsal cilia usually less dense than those on ventral surface..... Family 1 Nassulidae

Ciliation incomplete; dorsal surface without cilia or with a few sensory bristles

Posterior ventral surface with a style.....
..... Family 2 Dysteriidae (p. 523)

Without a style..... Family 3 Chlamidodontidae (p. 525)

Furrow from anterior end of cytostome; parasitic.....
..... Family 4 Pycnothricidae (p. 528)

Family 1 **Nassulidae** Schouteden

Genus **Nassula** Ehrenberg. Oval to elongate; ventral surface flat, dorsal surface convex; usually brightly colored, due to food material; cytostome $1/3$ – $1/4$ from anterior end; body often bent to left near cytostome; opening of oral basket deep, in a vestibule with a membrane; macronucleus spherical or ovoid, central; a single micronucleus; contractile vacuole large, with accessory vacuoles and opens ventrally through a tubule-pore; fresh or salt water. Many species.

N. aurea E. (Fig. 240, *a*). 200– 250μ long; fresh and brackish water (Kahl).

Genus **Paranassula** Kahl. Similar in general appearance to *Nassula*; but with preoral and dorsal suture line; longer caudal cilia on dorsal suture; pharyngeal basket not funnel-like, with 16–18 trichites; about 75 ciliary rows; trichocysts especially in anterior region.

P. microstoma (Claparède et Lachmann) (Fig. 240, *b*). Pellicle roughened by a criss-cross of longitudinal and circular furrows; macronucleus elongate oval, posterior; contractile vacuole near

middle and right-dorsal; about 80–95 μ long; salt water, Florida (Noland).

Genus **Cyclogramma** Petty. Somewhat resembling *Nassula*; but conspicuous oral basket in pyriform depression and opens toward left on ventral surface; depression with a short row of small membranes at its anterior edge; trichocysts usually better developed than in *Nassula*; fresh water.

C. (Nassula) trichocystis (Stokes) (Fig. 240, *c*). Body colorless or slightly rose-colored; trichocysts thick and obliquely arranged; one contractile vacuole; usually full of blue-green food vacuoles; actively motile; about 60 μ long; in fresh water among algae.

Genus **Chilodontopsis** Blochmann. Elongate ellipsoid; colorless; ventral surface flattened, dorsal surface slightly convex; both sides ciliated; oral basket without vestibule; cytostome with a membranous ring; usually with a postoral ciliary furrow; fresh water.

C. (Chilodon) vorax (Stokes) (Fig. 240, *d*). Elongate ellipsoid; anterior region slightly curved to left; snout fairly distinct; oral basket with about 16 rods; several contractile vacuoles distributed, a large one terminal; macronucleus large, lenticular, granulated; with a closely attached micronucleus; 50–160 μ long; fresh water.

Genus **Eucamptocerca** da Cunha. Elongate; posterior part drawn out into a caudal prolongation; dorso-ventrally flattened; ciliation on both sides; round cytostome with basket in anterior ventral surface. One species.

E. longa de C. (Fig. 240, *e*). 300 μ by 25 μ ; macronucleus ovoid, with a micronucleus; contractile vacuole(?); in brackish water (salt contents 3 per cent); Brazil.

Genus **Orthodon** Gruber. Oval; contractile; colorless; much flattened; anterior region curved toward left; striation on both dorsal and ventral sides; cytostome toward right border; oral basket long; macronucleus oval; contractile vacuole terminal; fresh or salt water.

O. hamatus G. (Fig. 240, *f*). Extended 20–260 μ long, contracted 90–150 μ long; flask-shaped; oral basket with 16 trichites; salt water.

Family 2 Dysteriidae Kent

Genus **Dysteria** Huxley (*Ervilia*, Dujardin; *Iduna*, *Aegyria*, Claparède et Lachmann; *Cypridium*, Kent). Ovate; dorsal sur-

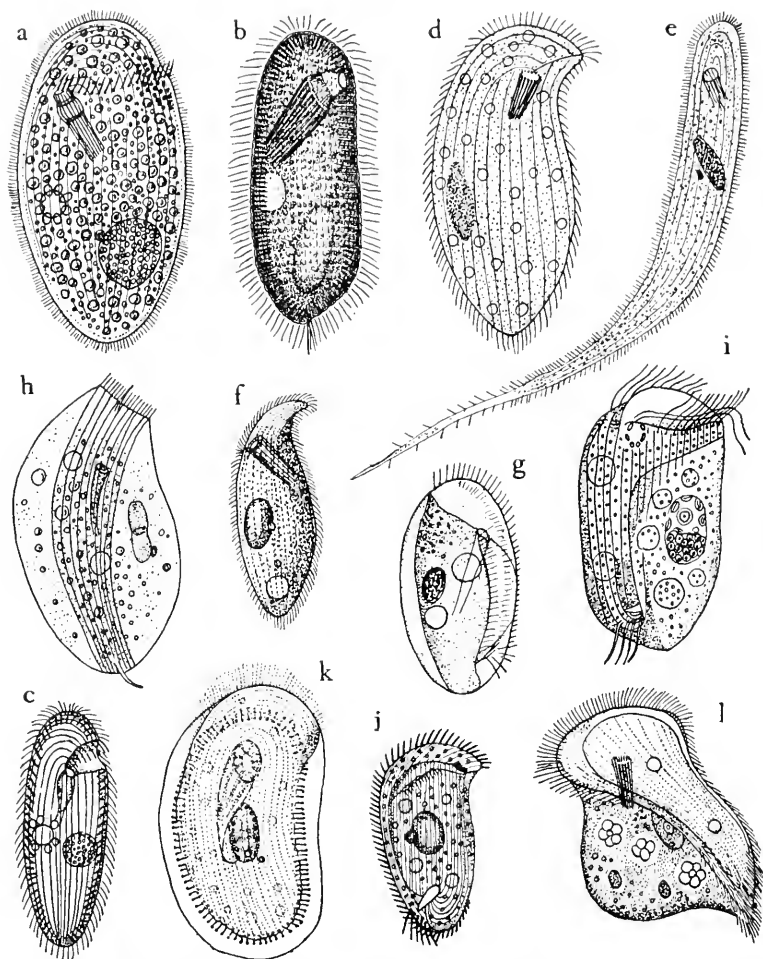


FIG. 240. a, *Nassula aurea*, $\times 190$ (Schewiakoff); b, *Paranassula microstoma*, $\times 400$ (Noland); c, *Cyclogramma trichocystis*, $\times 510$ (Stokes); d, *Chilodontopsis vorax*, $\times 200$ (Stokes); e, *Eucamptocerca longa*, $\times 320$ (da Cunha); f, *Orthodon hamatus*, $\times 160$ (Entz); g, *Dysteria culkinsi*, $\times 540$ (Calkins); h, *Trochilia palustris*, $\times 1070$ (Roux); i, *Trochilioides recta*, $\times 740$ (Kahl); j, *Hartmannula entzi*, $\times 220$ (Entz); k, *Chlamidodon mnemosyne*, $\times 520$ (MacDougall); l, *Phascolodon vorticella*, $\times 340$ (Stein).

face convex, ventral surface flat or concave; left ventral side with non-ciliated ventral plate; postoral ciliation is continuation of preoral to right of cytostome and parallel to right margin; cyto-

stome in a furrow near right side; posterior style or spine conspicuous; macronucleus spheroid or ovoid, central; with a micronucleus; usually 2 contractile vacuoles; fresh or salt water. Numerous species.

D. calkinsi Kahl (Fig. 240, *g*). About 45μ by 27μ ; salt water; Woods Hole.

Genus **Trochilia** Dujardin. Similar to *Dysteria*; but ciliated right ventral side free; fresh or salt water. Several species.

T. palustris Stein (Fig. 240, *h*). 25μ long; fresh water.

Genus **Trochilioides** Kahl. Rounded at anterior end, narrowed posteriorly; right side more convex than left; cytostome anterior with cytopharynx and preoral membrane; conspicuous longitudinal bands on right half with longitudinal striae, becoming shorter toward left; fresh or salt water.

T. recta K. (Fig. 240, *i*). $40\text{--}50\mu$ long; sapropelic in fresh and brackish water.

Genus **Hartmannula** Poche (*Onchodactylus* Entz). Ventral surface uniformly ciliated; cytopharynx with short rods; in salt water.

H. cntzi Kahl (Fig. 240, *j*). $80\text{--}140\mu$ long; salt water.

Family 3 Chlamidodontidae Claus

Genus **Chlamidodon** Ehrenberg. Ellipsoid, reniform, elongate triangular, etc.; cilia only on ventral surface, anterior cilia longer; cytostome elongate oval and covered with a membrane bearing a slit; oral basket made up of closely arranged rods with apical processes; along lateral margin, there is a characteristic striped band which is a canalicule of unknown function; fresh or salt water.

C. mnemosyne E. (Fig. 240, *k*). Ellipsoid or reniform; right side convex, left side concave; ventral side flat, dorsal side greatly convex; a band of trichites, 'railroad track,' parallel to body outline; oral basket with 8–10 rods; macronucleus oval; 4–5 contractile vacuoles distributed; $60\text{--}90\mu$ long; salt water. MacDougall (1928) observed it in the brackish water at Woods Hole and studied its neuromotor system.

Genus **Phascolodon** Stein. Ovoid; with broad anterior end and bluntly pointed posterior end; ventral side concave or flat, dorsal side convex; ciliated field on ventral surface narrowed laterally behind cytostome, forming V-shaped ciliary area (about 12 rows);

cytostome ellipsoid with oral basket; macronucleus oval with a micronucleus; 2 contractile vacuoles; fresh water.

P. vorticella S. (Fig. 240, *l*). 80–110 μ long, cytostome covered by a slit-bearing membrane; with 2 preoral membranes; fresh water.

Genus **Cryptopharynx** Kahl. Ellipsoid, anterior third bent to left; ventral surface flat, dorsal surface with hump; spiral inter-ciliary furrows ridged; oval cytostome at anterior end; no cytopharynx; dorsal hump yellowish, granulated with gelatinous cover; 2 macronuclei; 1 micronucleus; 2 contractile vacuoles, one posterior and the other toward left side at bend of body. One species.

C. setigerus K. (Fig. 241, *a, b*). Elongate ellipsoid; anterior region bent to left; ventral surface flat, dorsal surface with a hump; about 15 ventral ciliary rows; 2 vesicular macronuclei and 1 micronucleus, dorso-central; 33–96 μ by 21–45 μ (Kirby). Kirby found the organism in salt marsh pools (salinity 1.2–9.7 per cent) with purple bacteria in California.

Genus **Chilodonella** Strand (*Chilodon* Ehrenberg). Ovoid; dorso-ventrally flattened; dorsal surface convex, ventral surface flat; ventral surface with ciliary rows; anteriorly flattened dorsal surface with a cross-row of bristles; cytostome round; oral basket conspicuous, protrusible; macronucleus rounded; contractile vacuoles variable in number; fresh or salt water or ecto-commensal on fish and amphipods. Many species.

C. cucullulus (Müller) (*Chilodon steini* Blochmann) (Figs. 50; 241, *c-e*). 19–20 ventral ciliary rows; oral basket with about 12 rods and with 3 preoral membranes; macronucleus oval, a characteristic concentric structure; micronucleus small; body 100–300 μ long, most often 130–150 μ long; fresh and brackish water.

C. caudata (Stokes) (Fig. 241, *f*). About 42 μ long; standing water.

C. fluviatilis (S.) (Fig. 241, *g*). About 50 μ long; fresh water.

C. uncinata (Ehrenberg) (Fig. 81). 50–90 μ long; about 11 ventral ciliary rows; some 7 dorsal bristles; widely distributed in various freshwater bodies; several varieties. MacDougall (1925) studied conjugation and mutation (p. 164) of this organism.

C. cyprini (Moroff) (Fig. 241, *h*). 50–70 μ by 30–40 μ ; in integument and gills of cyprinoid fishes; the organism, if freed from the host body, dies in 12–24 hours.

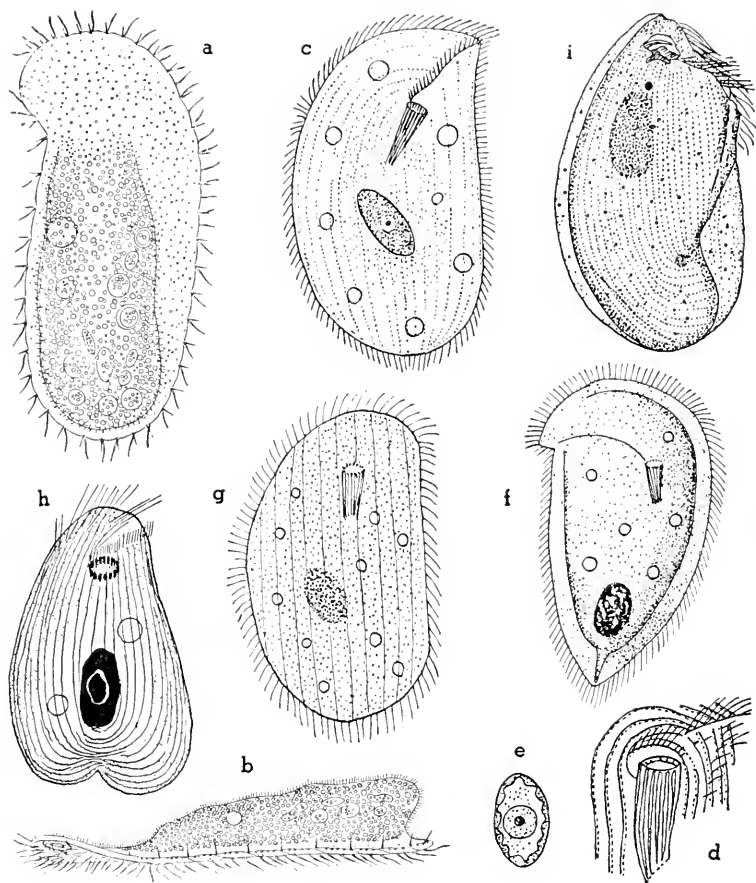


FIG. 241. a, b, *Cryptopharynx setigerus*, $\times 650$ (Kirby); c-e, *Chilonella cucullulus* (c, $\times 270$ (Stein); d, oral region; e, nucleus (Penard)); f, *C. caudata*, $\times 1000$ (Stokes); g, *C. fluviatilis*, $\times 800$ (Stokes); h, *C. cyprini*, $\times 670$ (Moroff); i, *Allosphaerium palustris*, $\times 1000$ (Kidder and Summers).

C. longipharynx Kidder et Summers. $17-21\mu$ (average 19μ) long; cytopharynx long, reaches posterior end; ectocommensal on amphipods, *Talorchestia longicornis* and *Orchestia palustris*; Woods Hole.

C. hyalina K. et S. 40μ ($36-47\mu$) long; ectocommensal on *Orchestia agilis*; Woods Hole.

C. rotunda K. et S. 29μ ($27-34\mu$) long; ectocommensal on *Orchestia agilis*; Woods Hole.

Genus **Allosphaerium** Kidder et Summers. Oval; right side concave, left side more or less flat; body highly flattened; arched dorsal surface devoid of cilia; ventral surface slightly concave with 12–27 ciliary rows; right and left margins of ventral surface with a pellicular fold; cytostome anterior-ventral, oval or irregular, surrounded by ridge on posterior border, extending to left margin; in front of it the peristome; 3 groups of ciliary membranes extending out of cytostome; macronucleus oval, central or anterior; a micronucleus; 2 (or 1) contractile vacuoles; a refractile spherule regularly present in posterior portion of endoplasm; ectoecommensal on carapace and gills of amphipods.

A. palustris K. et S. (Fig. 241, *i*). 46–59 μ long; 27 ventral ciliary rows; on *Orchestia palustris* and *Talorchestia longicornis*; Woods Hole.

A. sulcatum K. et S. 24–32 μ long; 12 ciliary rows; on carapace of *Orchestia agilis* and *O. palustris*; Woods Hole.

A. granulatum K. et S. 32–42 μ long; rotund; 17 ciliary rows; cytoplasm granulated; on carapace of *Orchestia agilis* and *O. palustris*; Woods Hole.

A. caudatum K. et S. Resembles *A. palustris*; 35–45 μ long; 14 ciliary rows; 1 contractile vacuole; ectoplasm at posterior end, drawn out into a shelf; on *Orchestia agilis*; Woods Hole.

A. convexa K. et S. 24–36 μ long; 17 ciliary rows; on carapace and gill lamellae of *Talorchestia longicornis*; Woods Hole.

Family 4 **Pycnothricidae** Poche

Ciliation uniform; ectoplasm thick and conspicuous; a furrow or groove connects the cytostome with the anterior end; parasitic in alimentary canal of mammals.

Genus **Pycnothrix** Schubotz. Large, elongate; with broadly rounded anterior and narrowed posterior end; somewhat flattened; short thick cilia throughout; ectoplasm thick; macronucleus spherical, in anterior 1/6; micronucleus(?); 2 longitudinal grooves, one beginning on each side near anterior end, united at the notched posterior end; a series of apertures in grooves considered as cytostomes; at posterior 1/3, a pore gives rise to branching canals running through endoplasm, and is considered as excretory in function; in colon of *Procapra capensis* and *P. brucci*. One species.

P. monocystoides S. (Fig. 242, *a*). 300 μ –2 mm. long.

Genus **Nicollella** Chatton et Pérard. Elongate; a narrow groove extends from the anterior end to cytostome, located at middle of body; bilobed posteriorly; contractile vacuole terminal; macronucleus ellipsoid, anterior; a micronucleus; ectoplasm thick

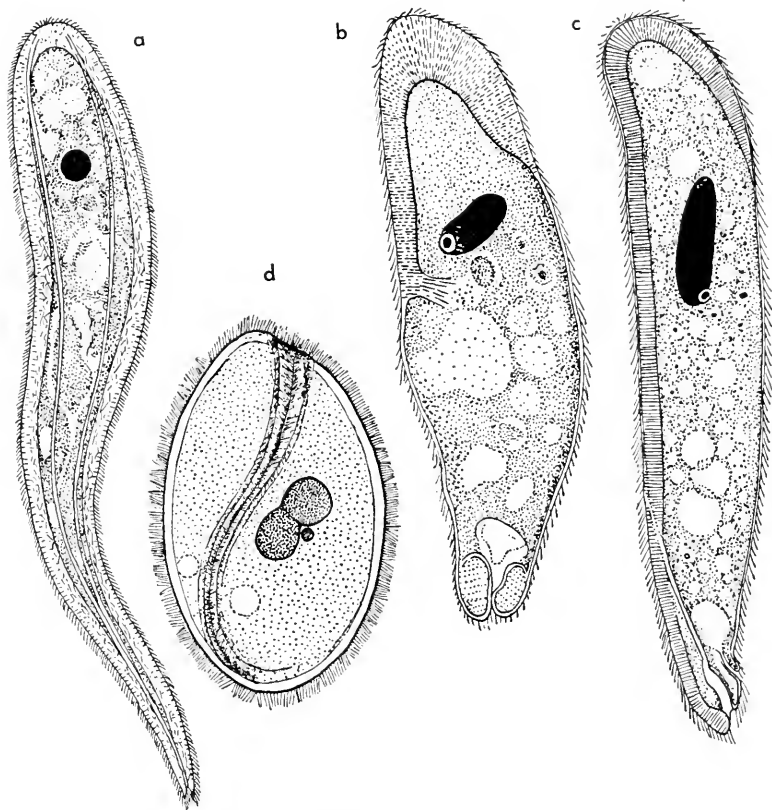


FIG. 242. a, *Pycnothrix monocystoides*, $\times 50$ (Chatton and Pérard); b, *Nicollella ctenodactyli*, $\times 170$ (Chatton and Pérard); c, *Collinella gundi*, $\times 170$ (Chatton and Pérard); d, *Buxtonella sulcata*, $\times 400$ (Jameson).

anteriorly; ciliation uniform; in colon of *Ctenodactylus gundi*. One species.

N. ctenodactyli C. et P. (Fig. 242, b). 70–550 μ by 40–150 μ .

Genus **Collinella** Chatton et Pérard. More elongate than *Nicollella*; uniform ciliation; a groove extends from end to end; cytostome at posterior end of the groove; contractile vacuole

terminal; macronucleus much elongated, central or posterior; in colon of *Ctenodactylus gundi*.

C. gundi C. et P. (Fig. 242, *c*). 550–600 μ by 100 μ .

Genus **Buxtonella** Jameson. Ovoid; a prominent curved groove bordered by 2 ridges from end to end; cytostome at anterior end; ciliation uniform; in caecum of cattle. One species.

B. sulcata J. (Fig. 242, *d*). 55–124 μ by 40–72 μ .

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CHAPTER 33

Order 1 **Holotricha** Stein (continued)

Suborder 3 **Trichostomata** Bütschli

- With gelatinous lorica; swimming backward.....
..... Family 1 Marynidae (p. 532)
- Without lorica
 - Compressed; armor-like pellicle; ciliation sparse, mainly on flat right side in 2–9 broken rows on semicircular or crescentic keel; cytostome on flattened ventral surface, with an obscure membrane..... Family 2 Trichopelmidae (p. 532)
 - Body form and ciliation otherwise
 - With a long caudal cilium; cilia in 3–4 spiral rows on anterior half, very small forms..... Family 3 Trimyemidae (p. 534)
 - Without a caudal cilium; form and ciliation otherwise
 - With a spiral zone of special cilia, from cytostome to posterior end
 - Spiral zone extends from anterior right to posterior left....
..... Family 4 Spirozonidae (p. 534)
 - Spiral zone extends from anterior left to posterior right....
..... Family 5 Trichospiridae (p. 534)
 - Without spiral zone of special cilia
 - Ciliated cross-furrow in anterior 1/5 on ventral surface, leads to cytostome..... Family 6 Plagiopylidae (p. 534)
 - Without ciliated cross-furrow
 - Cytostome in flat oval groove with heavily ciliated ridge in anterior 1/4..... Family 7 Clathrostomidae (p. 536)
 - Cytostome funnel-like, deeply situated
 - Cytostomal funnel with strong cilia; peristome from anterior left to middle right.....
..... Family 8 Parameciidae (p. 537)
 - Without such a peristome
 - Free-living; oral funnel deep; cilia at bottom and top.....
..... Family 9 Colpodidae (p. 540)
 - Endozoic
 - Commensal in vertebrates.....
..... Family 10 Entorhipidiidae (p. 541)
 - Parasitic in vertebrates
 - Ciliation uniform
 - With concretment vacuoles.....
..... Family 11 Paraisotrichidae (p. 543)
 - Without the vacuoles.....
..... Family 12 Isotrichidae (p. 544)

Ciliation not uniform

Cytostome occupies the entire anterior end;
cilia only in anterior region.....

..... Family 13 Cyathodiniidae (p. 544)

Cytostome not terminal; tufts of cilia above
and below cytostome and in posterior
region.....

..... Family 14 Blepharocoridae (p. 544)

Family 1 **Marynidae** Poche

Genus **Maryna** Gruber. Peristome makes a complete circle, thus the cone is entirely separated from anterior edge of body; cytostome left ventral, elongate slit; ridge also with a slit; gelatinous lorica, dichotomous.

M. socialis G. (Fig. 243, *a, b*). About 150 μ long; in infusion made from long-dried mud.

Genus **Mycterothrix** Lauterborn (*Trichorhynchus* Balbiani). Anterior cone continuous on dorsal side with body ridge; hence free edge of body only on ventral side; no ventral slit.

M. erlangeri L. (Fig. 243, *c*). Nearly spherical with zoochlorellae; 50–55 μ by 40–50 μ ; fresh water.

Family 2 **Trichopelmidae** Kahl

Genus **Trichopelma** Lavender. Compressed; surface with longitudinal furrows, seen as lines in end-view; coarse ciliation throughout; cytostome toward left edge about 1/3 from the anterior end; cytopharynx tubular; macronucleus spheroid, central; 2 contractile vacuoles; fresh water.

T. sphagnetorum (L.) (Fig. 243, *d*). 25–40 μ long; in fresh water.

Genus **Pseudomicrothorax** Mermod (*Craspedothorax* Sondheim). More or less compressed; cytostome opens in anterior half toward left side, in a depression surrounded by ciliary rows; body surface marked with a broad longitudinal ridge with cross striation; furrows canal-like; cilia on ventral side; cytopharynx tubular, with elastic rods; fresh water.

P. agilis M. (Fig. 243, *e, f*). Ellipsoid; 48–58 μ long; in fresh water.

Genus **Drepanomonas** Fresenius (*Drepanoceras* Stein). Highly flattened; aboral surface convex; oral surface flat or concave; with a few deep longitudinal furrows; ciliation sparse; cytostome and a small cytopharynx simple, near the middle of body; fresh water. Several species.

D. dentata F. (Fig. 243, g). With a small process near cytostome; 2 rows of ciliary furrows on both oral and aboral surfaces; cilia on both ends of oral surface; 40–65 μ long; in fresh water.

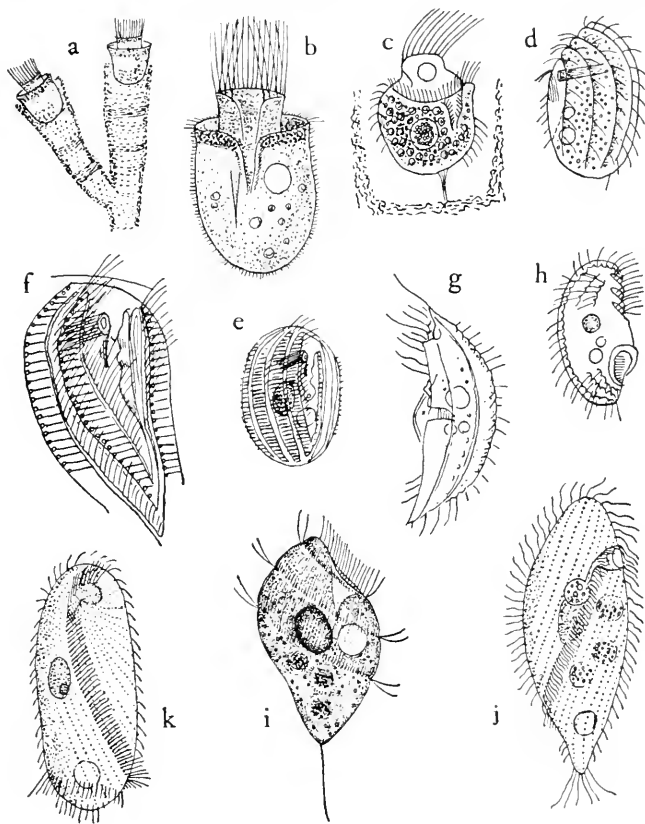


FIG. 243. a, b, *Maryna socialis* (a, $\times 40$; b, $\times 160$) (Gruber); c, *Myceterothrix erlangeri*, $\times 310$ (Kahl); d, *Trichopelma sphagnetorum*, $\times 570$ (Kahl); e, f, *Pseudomicrothorax agilis* (e, $\times 340$; f, $\times 670$) (Kahl); g, *Drepanomonas dentata*, $\times 540$ (Penard); h, *Microthorax simulans*, $\times 620$ (Kahl); i, *Trimyema compressum*, $\times 410$ (Lackey); j, *Spirozona caudata*, $\times 370$ (Kahl); k, *Trichospira inversa*, $\times 360$ (Kahl).

Genus **Microthorax** Engelmann (*Kreyella* Kahl). Small, flattened; with delicate keeled armor which is more or less pointed anteriorly and rounded posteriorly; ventral armor with 3 ciliary rows; oral depression posterior-ventral, with a stiff ectoplasmic lip on right side, below which there is a small membrane, and

with a small tooth on left margin; no cytopharynx; macronucleus spherical; 2 contractile vacuoles; in fresh water. Many species.

M. simulans Kahl (Fig. 243, *h*). 30–35 μ long; decaying plant infusion, also in moss.

Family 3 Trimyemidae Kahl

Genus **Trimyema** Lackey (*Sciadostoma* Kahl). Ovoid, more or less flattened; anterior end bluntly pointed, posterior end similar or rounded; with a long caudal cilium; cilia on 3–4 spiral rows which are usually located in the anterior half of body; round cytostome near anterior end with a small cytopharynx; spherical macronucleus central with a small micronucleus; one contractile vacuole; active swimmer; fresh or salt water.

T. compressum L. (Fig. 243, *i*). About 65 μ by 35 μ ; Lackey found it in Imhoff tank; fresh and salt water (Kahl); Klein (1930) studied its silverline system.

Family 4 Spirozonidae Kahl

Genus **Spirozona** Kahl. Short spindle-form; anterior end truncate, posterior region drawn out to a rounded end, with a group of longer cilia; spiral ciliation; beginning at right posterior end the central ciliary row runs over ridge to left and then reaches the cytostome; other rows are parallel to the above; cytostome in anterior 1/4, with cytopharynx; ellipsoid macronucleus nearly central; contractile vacuole terminal; fresh water, sapropelic.

S. caudata K. (Fig. 243, *j*). 80–100 μ long.

Family 5 Trichospiridae Kahl

Genus **Trichospira** Roux. Body cylindrical; posterior end rounded, anterior end conical in profile, where the cytostome surrounded by 2 spiral rows of cilia, is located; a special ciliary band beginning in the cytostomal region runs down on ventral side, turns spirally to left and circles partially posterior region of body; ciliary rows parallel to it; macronucleus oval, with a micronucleus; contractile vacuole posterior; fresh water, sapropelic.

T. inversa (Claparède et Lachmann) (Fig. 243, *k*). 70–100 μ long.

Family 6 Plagiopylidae Schewiakoff

Genus **Plagiopyla** Stein. Peristome a broad ventrally opened groove from which body ciliation begins; peristomal cilia short,

except a zone of longer cilia at anterior end; cytostome near median line at the end of the peristome; cytopharynx short; a peculiar 'stripe band' located on dorsal surface has usually its origin in the peristomal groove, after taking an anterior course for a short distance, curves back and runs down posteriorly near right edge and terminates about $1/3$ the body length from posterior end; macronucleus rounded; a micronucleus; contractile vacuole terminal; free-living or endozoic.

P. nasuta S. (Fig. 244, a). Ovoid; tapering anteriorly; peristome at right angles or slightly oblique to the edge; trichocysts at right angles to body surface; macronucleus round to irregular in shape; body about 100μ (80 – 180μ) long; sapropelic in brackish water. Lynch (1930) observed this ciliate in salt water cultures in California and found it to be 70 – 114μ by 31 – 56μ by 22 – 37μ .

P. minuta Powers (Fig. 244, b). 50 – 75μ by 36 – 46μ ; in intestine of *Strongylocentrotus droebachiensis*; the Bay of Fundy.

Genus **Lechriopyla** Lynch. Similar to *Plagiopyla*; but with a large internal organella, furcula, embracing the vestibule from right, and a large crescentic motorium at left end of peristome; in the intestine of sea-urchins.

L. mystax L. (Fig. 244, c). 113 – 174μ long; in gut of *Strongylocentrotus purpuratus* and *S. franciscanus*; California.

Genus **Sonderia** Kahl. Similar to *Plagiopyla* in general appearance; ellipsoid; flattened; peristome small and varied; body covered by 2 – 4μ thick gelatinous envelope which regulates osmosis, since no contractile vacuole occurs (Kahl); with or without a striped band; trichocysts slanting posteriorly; in salt or brackish water. Kirby (1934) showed that several species of the genus are common in the pools and ditches in salt marshes of California, salinities of which range 3.5 – 10 per cent or even up to 15 – 20 per cent.

S. pharyngea Kirby (Fig. 244, d). Ovoid to ellipsoid; flattened; 84 – 110μ by 48 – 65μ ; gelatinous layer about 2μ thick, with bacteria; about 60 longitudinal ciliary rows, each with 2 borders; peristome about 35μ long, at anterior end, oblique; with closely set cilia from the opposite inner surfaces; cytopharynx conspicuous; spherical macronucleus anterior, with a micronucleus; trichocysts (7 – 9μ long) distributed sparsely and unevenly, oblique to body surface; a group of bristle-like cilia at posterior end; often brightly colored because of food material; in salt marsh, California.

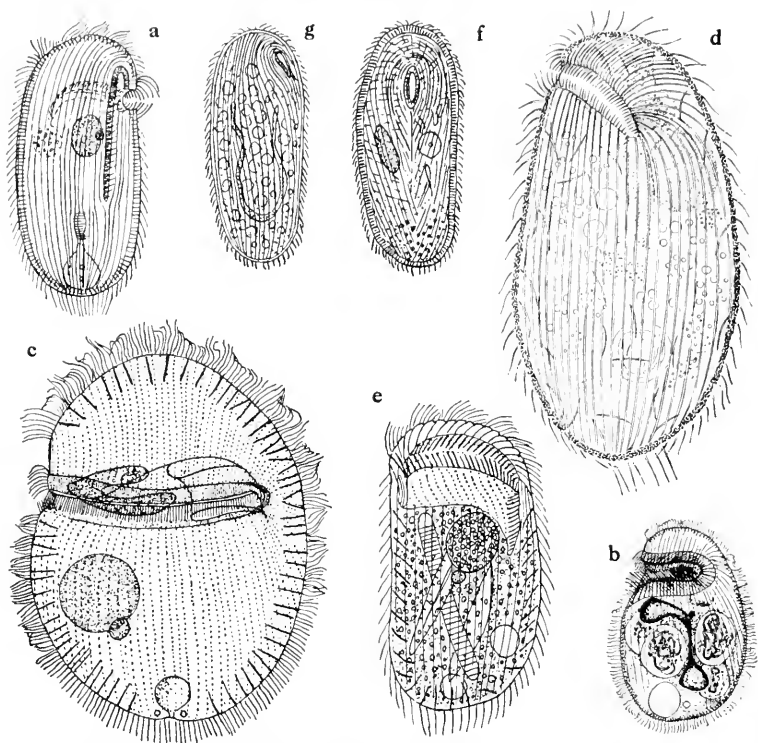


FIG. 244. a, *Plagiopyla nasuta*, $\times 340$ (Kahl); b, *P. minuta*, $\times 400$ (Powers); c, *Lechriopyla mystax*, $\times 340$ (Lynch); d, *Sonderia pharyngea*, $\times 590$ (Kirby); e, *S. vorax*, $\times 310$ (Kahl); f, *Clathrostoma viminale*, $\times 220$ (Penard); g, *Physalophrya spumosa*, $\times 160$ (Penard).

S. vorax Kahl (Fig. 244, e). Broadly ellipsoid; size variable, $70\text{--}180\mu$ long; ventral surface flattened; posterior border of peristomal cavity extending anteriorly; in salt marsh; California (Kirby).

Family 7 *Clathrostomidae* Kahl

Genus *Clathrostoma* Penard. Ellipsoid; with an oval pit in anterior half of the flattened ventral surface, in which occur 3–5 concentric rows of shorter cilia; cytostome a long slit located at the bottom of this pit; with a basket composed of long fibrils on the outer edge of pit; in fresh water.

C. viminale P. (Fig. 244, f). Resembles a small *Frontonia leucas*; macronucleus short sausage-form; 4 micronuclei in a com-

paet group; endoplasm with excretion crystals; 5 preoral ciliary rows; 130–180 μ long; in fresh water.

Family 8 **Parameciidae** Grobben

Genus **Paramecium** Hill (*Paramaccium* Müller). Cigar-shaped; circular or ellipsoid in cross-section; with a single macronucleus and 1 to many vesicular or compact micronuclei; peristome long, broad, and conspicuous; in fresh or brackish water. Several species.

P. caudatum Ehrenberg (Figs. 22, *e*; 35; 39, *a–e*; 48; 74; 245, *a*). 200–260 μ long; with a compact micronucleus, a massive macronucleus; 2 contractile vacuoles on aboral surface; posterior end bluntly pointed; in fresh water. The most widely distributed species.

P. aurelia Müller (Figs. 77; 79; 245, *b*). 120–250 μ long; 2 small vesicular micronuclei, a massive macronucleus; 2 contractile vacuoles on aboral surface; posterior end more rounded than *P. caudatum*; in fresh water.

P. multimicronucleata Powers et Mitchell (Figs. 19; 20; 28; 29; 245, *c*). Slightly larger than *P. caudatum*; 3–7 contractile vacuoles; 4 or more vesicular micronuclei; a single macronucleus; in fresh water.

P. bursaria (Ehrenberg) (Fig. 245, *d*). Foot-shaped, somewhat compressed; about 100–200 μ by 50–60 μ ; with zoochlorellae as symbionts; micronucleus compact; 2 contractile vacuoles; in fresh water.

P. putrinum Claparède et Lachmann (Fig. 245, *e*). Similar to *P. bursaria*, but a single contractile vacuole and an elongated macronucleus; no zoochlorellae; 80–150 μ long; in fresh water.

P. calkinsi Woodruff (Fig. 245, *f*). Foot-shaped; posterior end broadly rounded; 100–130 μ by 50 μ ; 2 vesicular micronuclei; 2 contractile vacuoles; rotation of body clockwise when viewed from posterior end; in fresh and brackish water.

P. trichium Stokes (Fig. 245, *g*). Oblong; somewhat compressed; 70–100 μ long; micronucleus compact; 2 contractile vacuoles deeply situated, each with a convoluted outlet; in fresh water.

P. polycaryum Woodruff et Spencer (Fig. 245, *h*). Form similar to *P. bursaria*; 70–110 μ long; 2 contractile vacuoles; 3–8 vesicular micronuclei; in fresh water.

P. woodruffi Wenrich (Fig. 245, *i*). Similar to *P. polycaryum*;

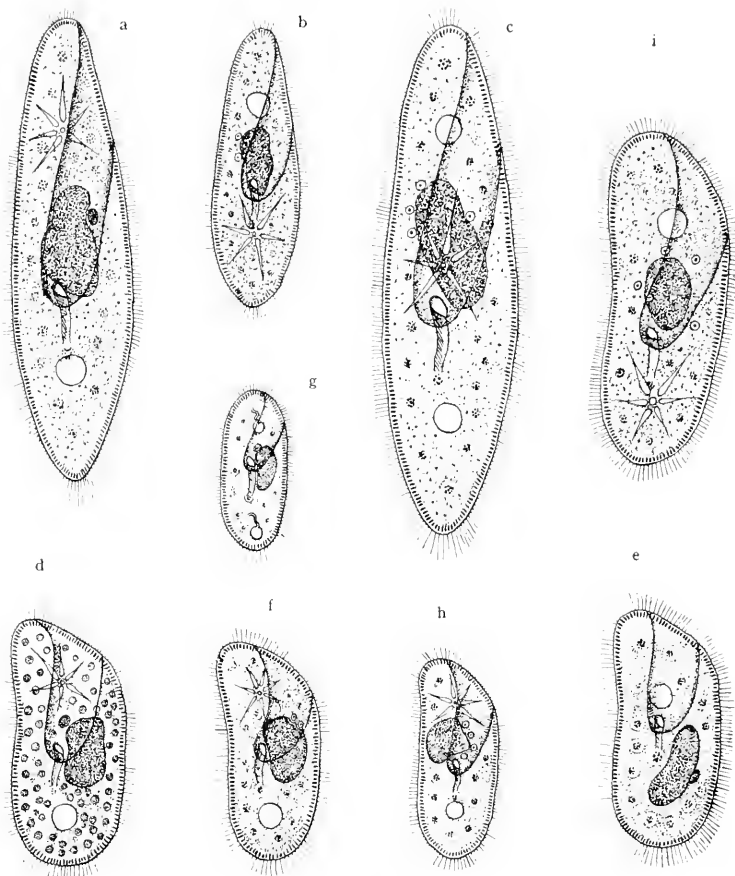


FIG. 245. Semi-diagrammatic drawings of nine species of *Paramecium* in oral surface view, showing distinguishing characteristics taken from fresh and stained specimens, $\times 230$ (several authors). a, *P. caudatum*; b, *P. aurelia*; c, *P. multimicronucleata*; d, *P. bursaria*; e, *P. putrinum*; f, *P. calkinsi*; g, *P. trichium*; h, *P. polycaryum*; i, *P. woodruffi*.

150–210 μ long; 2 contractile vacuoles; 3–4 vesicular micronuclei; brackish water.

Although *Paramecium* occurs widely in various freshwater bodies throughout the world and has been studied extensively by numerous investigators by mass or pedigree culture method, there are only a few observations concerning the process of encystment. Bütschli considered that *Paramecium* was one of the Protozoa

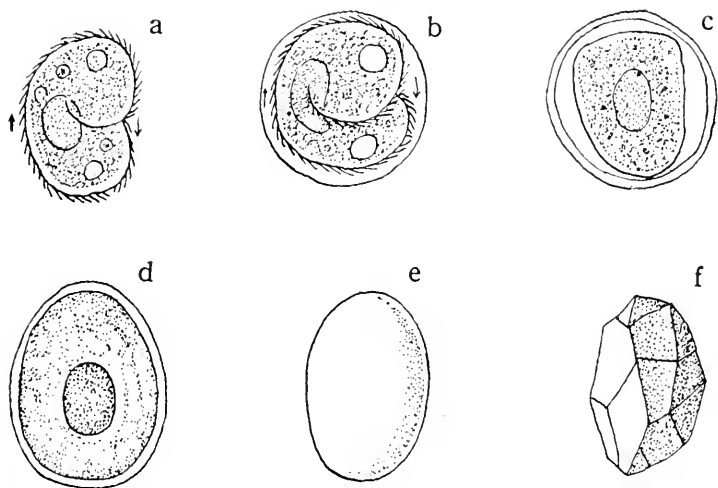


FIG. 246. a-c, encystment in a species of *Paramecium* (Curtis and Guthrie); d-f, encystment of *P. caudatum*, $\times 380$ (Michelson).

in which encystment did not occur. Stages in encystment were observed in *P. bursaria* (by Prowazek) and in *P. putrinum* (by Lindner). In recent years, four observers recorded their findings on the encystment of *Paramecium*. Curtis and Guthrie (1927) give figures in their textbook of zoology, showing the process (of *P. caudatum*?) (Fig. 246), while Cleveland (1927) injected *Paramecium* culture (species not mentioned) into the rectum of frogs and observed that the ciliate encysted within a thin membrane. Michelson (1928) found that if *P. caudatum* is kept in Knop-agar medium, the organism becomes ellipsoidal under certain conditions, later spherical to oval, losing all organellae except the nuclei, and develops a thick membrane; the fully formed cyst is elongated and angular, and resembles a sand particle (Fig. 246). Michelson considers its resemblance to a sand grain as the chief cause of the cyst having been overlooked by workers. In all these cases, however, it may be added that excystment has not been established.

Genus **Physalophrya** Kahl. Without peristome; but cytostome located near the anterior half of body, resembles much that of *Paramecium*; although there is no membrane, a ciliary row occurs in the left dorsal wall of cytopharynx; in fresh water. Taxonomic status is not clear; but because of its general resemblance to

Paramecium, the genus with only one species is mentioned here.

P. spumosa (Penard) (Fig. 244, *g*). Oval to cylindrical; highly plastic; cytoplasm reticulated; numerous contractile vacuoles; 150–320 μ long; in fresh water.

Family 9 Colpodidae Poche

Genus **Colpoda** Müller. Reniform; flattened; right border semi-circular; posterior half of left border often convex; oral funnel in the middle of flattened ventral side, but toward left border where depression occurs, which leads into peristome cavity and gives rise dorsally to a diagonal groove; left edge of cytostome bears a cross-striped ciliated area, but no protruding membrane as in *Bryophrya*; macronucleus spherical or oval, central; contractile vacuole terminal; in fresh water. Many species.

C. cucullus M. (Fig. 247, *a, b*). About 80 μ (50–120 μ) long; anterior keel with 8–10 indentations; macronucleus with a stellate endosome; trichocysts rod-form; food vacuoles dark; in fresh water with decaying plants and infusion.

C. inflata (Stokes) (Fig. 247, *c*). 50–80 μ long; anterior keel with 6–8 indentations; macronucleus similar to that of *C. cucullus*; in fresh water in vegetation.

C. californica Kahl (Fig. 247, *d*). About 30 μ long; highly flattened; cytostome small; protrichocysts very granular; cilia delicate, long, in a few rows; macronucleus with a stellate endosome; in moss; California.

C. steini Maupas. 25–45 μ long; 5–6 preoral ridges; in fresh water. Reynolds (1936) found that it adopts itself to various organs of the land slug, *Agriolimax agrestis*.

Genus **Tillina** Gruber. Similar to *Colpoda* in general appearance and structure; but cytopharynx a long curved, ciliated tube; in fresh water.

T. magna G. (Fig. 247, *e, f*). 180–200 μ long (Gruber); up to 400 μ long (Bresslau); macronucleus oval, with 6 micronuclei; contractile vacuole terminal, with 6 long collecting canals; in stagnant water and also coprozoic.

Genus **Bresslaua** Kahl. General body form resembles *Colpoda*; but cytopharynx large and occupies the entire anterior half.

B. vorax K. (Fig. 247, *g*). 80–120 μ long; in fresh water.

Genus **Bryophrya** Kahl. Ovoid to ellipsoid; anterior end more or less bent toward left side; cytostome median, about 1/3 from

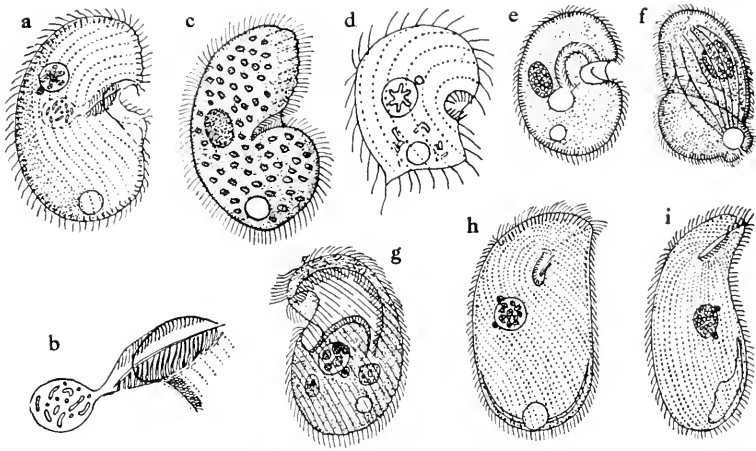


FIG. 247. a, b. *Colpoda cucullus* (a, $\times 340$; b, oral region) (Kahl); c, *C. inflata*, $\times 540$ (Stokes); d, *C. californica*, $\times 670$ (Kahl); e, f, *Tillina magna*, $\times 100$ (Bresslau); g, *Bresslauna vorax*, $\times 100$ (Kahl); h, *Bryophrya bavariensis*, $\times 280$ (Kahl); i, *Woodruffia rostrata*, $\times 190$ (Kahl).

anterior end, its right edge continues in horseshoe form around the posterior end and half of the left edge; anterior portion of left edge of the cytostome with posteriorly directed membrane; macronucleus oval or spherical; micronuclei; in fresh water.

B. bavariensis K. (Fig. 247, h). 50–120 μ long.

Genus **Woodruffia** Kahl. Form similar to *Chilodonella* (p. 526); highly flattened snout bent toward left; cytostome, a narrow diagonal slit, its left edge with a membranous structure and its right edge with densely standing short cilia; macronucleus spherical, many (?) micronuclei; contractile vacuole flattened, terminal; in salt water.

W. rostrata K. (Fig. 247, i). 120–180 μ long; salt water culture with *Oscillatoria*.

W. metabolica Johnson et Larson. 85–400 μ long; division cysts 85–155 μ in diameter; resting cysts 40–62 μ in diameter; in fresh water pond; California.

Family 10 Entorhipidiidae Madsen

Genus **Entorhipidium** Lynch. Triangular in general outline; colorless; large (155–350 μ long); flattened; posterior end drawn out with a bristle; anterior end bent to left; cytostome in depression close to left anterior border, with long cilia; with or without

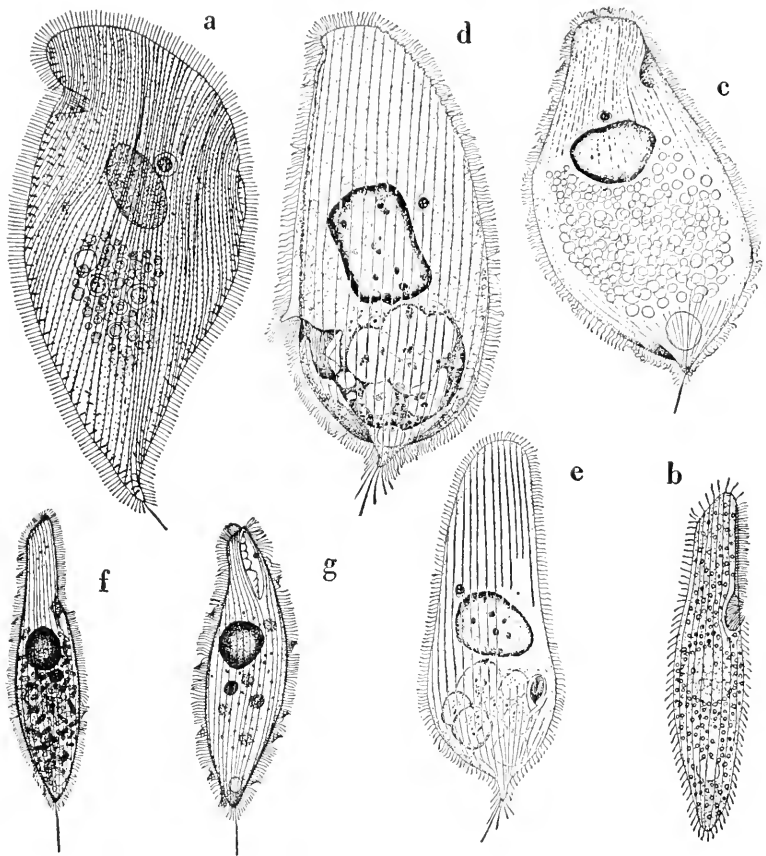


FIG. 248. a, *Entorhipidium echini*, $\times 270$ (Lynch); b, *Entodiscus indomitus*, $\times 380$ (Madsen); c, *E. borealis*, $\times 380$ (Powers); d, *Biggaria bermudense*, $\times 380$ (Powers); e, *B. echinometris*, $\times 380$ (Powers); f, *Anophrys elongata*, $\times 390$ (Powers); g, *A. aglycus*, $\times 390$ (Powers).

a cross-groove from preoral region; cytopharynx inconspicuous; trichocysts; macronucleus oval to sausage-form; 1 to several micronuclei; several (excretory) vacuoles left-ventral; in intestine of the starfish, *Strongylocentrotus purpuratus*. Four species.

E. echini L. (Fig. 248, a). About 253μ by 125μ ; California.

Genus **Entodiscus** Madsen. Broadly or narrowly lancelet-like, without narrowed posterior portion; cytostome small on left narrow side, about $2/5$ the body length from anterior end; without trichocysts; macronucleus central, with a micronucleus; con-

tractile vacuole subterminal; swimming movement rapid without interruption. Two species.

E. indomitus M. (Fig. 248, b). 80–117 μ by 20–23 μ ; in intestine of *Strongylocentrotus droebachiensis*.

E. borealis (Hentschel) (Fig. 248, c). Oval; cytostome nearer anterior end; 105–170 μ by 60–115 μ ; in gut of *Strongylocentrotus droebachiensis* and *Echinus esculentus*; Powers (1933) studied this species in the first-named host from Maine, and found a supporting rod which is imbedded in the margin along the right wall of the oral cavity and which he named *stomatostyle*.

Genus **Biggaria** Kahl. Scoop-like form; anterior 2/3 thin, posterior region thickened, terminating in a rudder-like style; cilia in longitudinal rows; longer cilia on caudal prolongation; cytostome in posterior half, opening into a vestibule, into which long cilia project from the roof; aperture to cytopharynx with 2 membranes; contractile vacuole subterminal; in the intestine of sea-urchins.

B. bermudense (Biggar) (Fig. 248, d). 90–185 μ by 48–82 μ ; in *Lytechinus variegatus*; Bermuda (Biggar), North Carolina (Powers); Powers (1935) found the organism further at Tortugas in *Lytechinus variegatus*, *Centrechinus antillarum*, *Echinometra lucunter*, *Tripneustes esculentus* and *Astrophyga magnifica*.

B. echinometris (B.) (Fig. 248, e). 80–195 μ by 33–70 μ ; in *Echinometris subangularis* (Bermuda) and *Lytechinus variegatus* (North Carolina).

Genus **Anophrys** Cohn. Cigar-shaped; flexible; longitudinal ciliary rows; peristome begins near the anterior end, parallel to body axis and about 1/3 the body length; a row of free cilia on right edge of peristome; cytostome inconspicuous; spherical macronucleus central; contractile vacuole terminal; in sea-urchins.

A. elongata Biggar (Fig. 248, f). About 96 μ long (Powers); 166 μ long (Biggar); in gut of *Lytechinus variegatus* and *Echinometris subangularis*; Bermuda (Biggar); Powers (1935) found this species also in the hosts mentioned for *Biggaria bermudense*.

A. aglycus Powers (Fig. 248, g). 56–120 μ by 16–35 μ ; in gut of *Centrechinus antillarum* and *Echinometra lucunter*; Tortugas.

Family 11 Paraisotrichidae da Cunha

Genus **Paraisotricha** Fiorentini. Uniformly ciliated in more or

less spiral longitudinal rows; longer cilia at anterior end; cytostome near anterior tip; contractile vacuole posterior; in caecum and colon of horse.

P. colpoidea F. (Fig. 249, a). 70–100 μ by 42–60 μ .

P. beckeri Hsiung (Fig. 249, b). 52–98 μ by 30–52 μ .

Family 12 **Isotrichidae** Bütschli

This family includes those forms which possess a thick pellicle and a dense ciliation.

Genus **Isotricha** Stein. Ovoid; flattened; dense longitudinal ciliary rows; cytostome at or near anterior end; several contractile vacuoles; reniform macronucleus and a micronucleus connected with, and suspended by, fibrils, karyophore; locomotion with posterior end directed forward; in stomach of cattle and sheep.

I. prostoma S. (Fig. 249, c). 80–195 μ by 53–85 μ .

I. intestinalis S. (Fig. 249, d). 97–130 μ by 68–88 μ .

Genus **Dasytricha** Schuberg. Oval, flattened; cilia in longitudinal spiral rows; no karyophore; in stomach of cattle.

D. ruminantium S. (Fig. 249, e). 50–75 μ by 30–40 μ .

Family 13 **Cyathodiniidae** da Cunha

Genus **Cyathodinium** da Cunha. Conical or pyriform; broad cytostome occupies the entire anterior end and extends posteriorly 1/4–3/4 the body length; deep with prominent ridges; oral cilia in a single row on left ridge; body cilia comparatively long, confined to anterior half; macronucleus round or ellipsoid; a micronucleus; 1 to several contractile vacuoles; in caecum and colon of guinea pigs.

C. conicum da C. Inverted cone; 50–80 μ by 20–30 μ ; in caecum of *Cavia aperca* and *C. porcella*.

C. piriforme da C. (Fig. 249, f). Typical form inverted pyriform; second form conical with tapering anterior end; contractile vacuole posterior; 30–40 μ by 20–30 μ ; in caecum of *Cavia aperca* and *C. porcella*; Lucas (1932) who made a cytological study of the organism, found some 52 per cent of guinea pigs which she examined in Philadelphia and St. Louis to harbor this ciliate.

Family 14 **Blepharocoridae** Hsiung

Elongate; cytostome anterior-ventral; cytopharynx long, cili-

ated; ciliary tufts at both ends; contractile vacuole terminal; in colon of horse or stomach of ruminants.

Genus **Blepharocorys** Bundle. Oral groove deep, near anterior end; 3 (oral, dorsal and ventral) ciliary zones at anterior end;

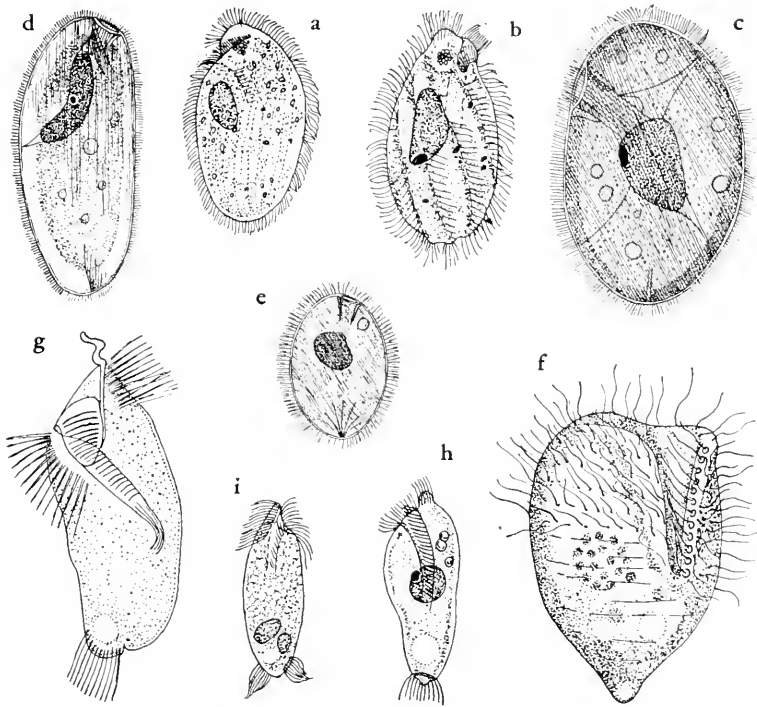


FIG. 249. a, *Paraisotricha colpoidea*, $\times 270$ (Hsiung); b, *P. beckeri*, $\times 360$ (Hsiung); c, *Isotricha prostoma*, $\times 500$ (Becker and Talbott); d, *I. intestinalis*, $\times 500$ (Becker and Talbott); e, *Dasytricha ruminantium*, $\times 330$ (Becker and Talbott); f, *Cyathodinium piriforme*, $\times 1290$ (Lucas); g, *Blepharocorys uncinata*, $\times 540$ (Reichenow); h, *B. bovis*, $\times 850$ (Dogiel); i, *Charon equi*, $\times 570$ (Hsiung).

caudal ciliary zone single; in caecum and colon of horse or stomach of cattle. Many species.

B. uncinata (Fiorentini) (*B. equi* Schumacher) (Fig. 249, g). With a screw-like anterior process; $55-74\mu$ by $22-30\mu$; in caecum and colon of horse.

B. bovis Dogiel (Fig. 249, h). $23-37\mu$ by $10-17\mu$; in stomach of cattle.

Genus **Charon** Jameson. Two caudal ciliary zones; in colon of horse or in stomach of ruminants.

C. equi Hsiung (Fig. 249, *i*). 30–48 μ by 10–14 μ ; in colon of horse.

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CHAPTER 34

Order 1 **Holotricha** Stein (continued)

Suborder 4 **Hymenostomata** Hickson

- Cytostome not connected with peristome.....
..... Family 1 **Frontoniidae**
- Cytostome at end or bottom of peristome
- Peristome sickle-form, ciliated slit; sunk at right angles to body surface..... Family 2 **Ophryoglenidae** (p. 555)
- Peristome long, begins at anterior end of body
- Peristome with a one-layered membrane which forms a pocket surrounding cytostome on right edge and a row of cilia or membrane on left..... Family 3 **Pleuronematidae** (p. 555)
- Peristome otherwise
- Peristome with 2 one-layered membranes; no distinct ectoplasmic pocket around cytostome.....
..... Family 4 **Cohnilembidae** (p. 558)
- Peristome furrow either covered densely with cilia, besides an undulating membrane on right edge, or with only a thick undulating membrane on the right edge.....
..... Family 5 **Philasteridae** (p. 559)

Family 1 **Frontoniidae** Kahl

Genus **Frontonia** Ehrenberg. Ovoid to ellipsoid; anterior end more broadly rounded than posterior end; flattened; oral groove lies in anterior third on more or less flattened ventral surface, to right of median line; lancet-like with pointed anterior and truncate posterior end; left edge more curved than right edge, and posteriorly becomes a prominent ectoplasmic lip; cytostome with a complex organization (on left edge a large undulating membrane composed of 3 layers, each being made up of 4 rows of cilia; on right, semi-membranous groups of cilia; 3 outer rows of cilia form the postoral suture; along this suture ectoplasm is discontinuous so that large food matter is taken in; with a small triangular ciliated field posterior to cytostome and left of suture); cytopharynx with numerous strong fibrils; ciliary rows close and uniform; ectoplasm with numerous fusiform trichocysts; macronucleus oval; 1 to many micronuclei; 1-2 contractile vacuoles, with collecting canals and an external pore; fresh or salt water. Many species.

F. leucas E. (Figs. 22, *a, b*; 250, *a*). 150–600 μ long; fresh water.

F. branchiostomae Codreanu (Fig. 250, *b*). 75–100 μ by 55–95 μ ; commensal in the branchial cavity of *Amphioxus*.

Genus **Disematostoma** Lauterborn. Somewhat similar to *Frontonia*; pyriform; with broadly rounded, truncate or concave anterior end and bluntly rounded narrow posterior end; preoral canal wide; a dorsal ridge in posterior region of body; macronucleus sausage-form; a micronucleus; contractile vacuole in middle of body toward left, with long collecting canals; in fresh water.

D. butschlii L. (Fig. 250, *c*). 135–155 μ long; with or without zoochlorellae; in fresh water.

Genus **Lembadion** Perty. Oval; dorsal side convex, ventral side concave; cytostome $3/4$ – $4/5$ the body length; on its left with a large membrane composed of many ciliary rows and on its right, numerous narrow rows of short free cilia; an undulating membrane and ciliary rows near posterior end; contractile vacuole in mid-dorsal region with a long tubule opening at posterior-right side; close ciliation uniform; macronucleus ellipsoid, subterminal; a micronucleus; long caudal cilia; in fresh water.

L. bullinum P. (Fig. 250, *d*). 120–200 μ long; posterior cilia 40–50 μ long.

Genus **Glaucoma** Ehrenberg (*Dallasia* Stokes). Ovoid or ellipsoid; ventral surface more or less flattened; dorsal surface convex; cytostome about $1/4$ the body length from anterior end, oblong or crescentic, with 3 undulating membranes; ectoplasmic ridge surrounds cytostome; ciliation and striation uniform; macronucleus rounded; a single micronucleus; with or without 1 or more caudal bristles; a single contractile vacuole; fresh water.

G. pyriformis E. (Fig. 250, *e*). Oval with short rounded anterior end; contractile vacuole near posterior end; somewhat flattened; cytostome near anterior end with a distinct membrane; cytopharynx short; body 45–55 μ by 30–40 μ (Schewiakoff); 38–80 μ long (Kahl); in fresh water. This ciliate has been reported to inhabit naturally and experimentally the body cavity of certain insects (p. 27–28).

G. frontata (Stokes). 65–140 μ long; in fresh water.

G. ficaria Kahl. 50–65 μ long; fig-like in form; a small ectoplasmic fringe; striae widely apart; contractile vacuole in posterior $1/5$ and right-dorsal; in fresh water.

Genus **Lambornella** Keilin. Ellipsoid; densely ciliated; close

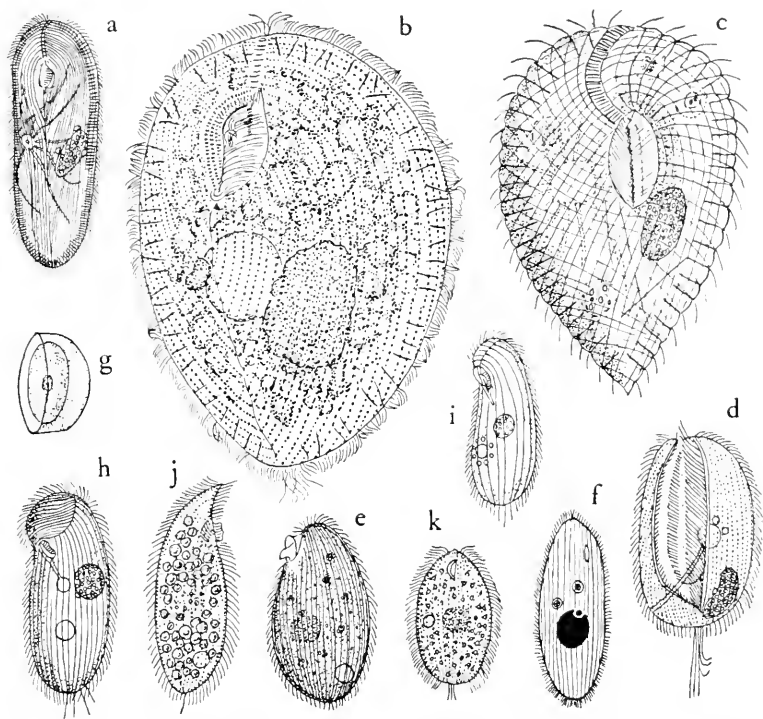


FIG. 250. a, *Frontonia leucas*, $\times 110$ (Kahl); b, *F. branchiostomae*, $\times 490$ (Codreanu); c, *Disematostoma butschlii*, $\times 340$ (Kahl); d, *Lembadion bullinum*, $\times 170$ (Kahl); e, *Glaucoma pyriformis*, $\times 380$ (Schewiakoff); f, g, *Lambornella stegomyiae*, $\times 340$ (Keilin); h, *Colpidium colpoda*, $\times 180$ (Kahl); i, *C. campylum*, $\times 150$ (Kahl); j, *Paraglaucoma rostrata*, $\times 400$ (Kahl); k, *Malacophrys rotans*, $\times 550$ (Kahl).

longitudinal striation; small oral pit in anterior half; macronucleus spherical; a micronucleus; cysts hemispherical; parasitic. One species.

L. stegomyiae K. (Fig. 250, f, g). $50-70\mu$ long; cysts $30-40\mu$ in diameter; in haemocoel of *Stegomyia scutellaris*.

Genus **Colpidium** Stein. Elongated; slightly flattened; dorsal surface more convex; cytostome $1/4$ from the anterior end on right side; preoral region curved to right; cytostome similar to *Glaucoma*; longitudinal striation close; macronucleus spherical; a micronucleus; a single contractile vacuole; fresh or salt water.

C. (Paramaccium) colpoda (Ehrenberg) (*Tillina helia* Stokes) (Figs. 10, c; 250, h). Ellipsoid; anterior end bent toward right;

preoral suture curves to left; macronucleus round; a micronucleus; body 100–150 μ long; in stagnant water and infusion.

C. (Tillina) campylum (Stokes) (Fig. 250, *i*). Ellipsoid to oval; ciliary furrows further apart than the last-named species; preoral suture not curved; 50–120 μ long; in fresh and brackish water.

C. striatum (Stokes). Similar to the last species; contractile vacuole further posterior; 50 μ long; in standing water.

Genus **Paraglaucoma** Kahl. Somewhat similar to *Glaucoma*; but without perioral ectoplasmic ridge; a membrane on right ridge of the cytostome; anterior end drawn out to a point in profile, posterior end rounded; a stiff posterior bristle; a contractile vacuole; rapid zig-zag movement. One species.

P. rostrata K. (Fig. 250, *j*). 60–80 μ long; in fresh water (often in dead rotiferan body); California, Wisconsin (Kahl).

Genus **Malacophrys** Kahl. Ellipsoid or cylindrical; plastic; cilia uniformly close-set in longitudinal rows; slit-like cytostome at anterior extremity; in fresh water.

M. rotans K. (Fig. 250, *k*). Oval; close and dense ciliation; spherical macronucleus central; a micronucleus; a single contractile vacuole; body 40–50 μ long; fresh water.

Genus **Espejoia** Bürger (*Balantiophorus* Penard). Ellipsoid; anterior end obliquely truncate; large cytostome at anterior end; postoral groove on ventral side, 1/4–1/3 the body length; a conspicuous membrane on the left edge of groove; in gelatinous envelope of eggs of insects and molluscs.

E. musicola (P.) (Fig. 251, *a*). Elongate; right side flat, left side convex; 80–100 μ long.

Genus **Cryptochilidium** Schouteden. Ellipsoid; with rounded anterior end, posterior end pointed in profile; highly compressed; uniform and close ciliation; cytostome near middle; one or more longer cilia at posterior end; contractile vacuole posterior; macronucleus round; a micronucleus; commensal.

C. echini Maupas (Fig. 252, *b*). 70–140 μ long; in gut of *Echinus lividus*.

Genus **Eurychilum** André. Elongate ellipsoid; anterior end somewhat narrowed; cilia short; dense ciliation not in rows; contractile vacuole terminal; macronucleus band-form; cytostome about 2/5 from anterior end and toward right, with a strong undulating membrane on left; no cytopharynx; actively swimming. One species.

E. actinae A. (Fig. 251, c). About 155μ long; in gastrovascular cavity of *Sagartia parasitica*.

Genus **Monochilum** Schewiakoff. Ovoid to ellipsoid; medium large; uniform and dense ciliation in rows; oblong cytostome left of median line, in about $1/4$ the body length from anterior end; short cytopharynx conical, with an undulating membrane; contractile vacuole near middle; in fresh water.

M. frontatum S. (Fig. 251, d). Anterior end broader; ventrally flattened, dorsally somewhat convex; macronucleus ellipsoid; a micronucleus; feeds on algae; 80μ by 30μ .

Genus **Dichilum** Schewiakoff. Similar to *Monochilum*; but membrane on both edges of the cytostome; in fresh or salt water.

D. cuneiforme S. (Fig. 251, e). Ellipsoid; cytostome about $1/5$ the body length from anterior end; right membrane larger than left; small cytopharynx; macronucleus ellipsoid; about 40μ by 24μ ; in fresh water.

Genus **Loxocephalus** Eberhard. Ovoid to cylindrical; often compressed; crescentic cytostome on slightly flattened area near anterior end, with 2 membranes; often a zone of cilia around body; usually 1 or more long caudal setae; endoplasm granulated, yellowish to dark brown; macronucleus ovoid; a single contractile vacuole; in fresh or brackish water. Many species.

L. plagiatus (Stokes) (Fig. 251, f). 50 – 65μ long; nearly cylindrical; 15–16 ciliary rows; endoplasm usually darkly colored; in fresh water among decaying vegetation.

Genus **Balanonema** Kahl. Similar to *Loxocephalus*; but with plug-like ends; cytostome difficult to see; a caudal seta; macronucleus oval; contractile vacuole; ciliation uniform or broken in the middle zone; fresh water.

B. biceps (Penard) (Fig. 251, g). Ellipsoid; no cilia in the middle region; contractile vacuole central; macronucleus posterior to it; 42 – 50μ long.

Genus **Platynematum** Kahl. Ovoid or ellipsoid; highly flattened; with a long caudal seta; contractile vacuole posterior-right; small cytostome more or less toward right side, with 2 outer membranes; ciliary furrows horseshoe-shaped; in fresh or salt water.

P. sociale (Penard) (Fig. 251, h). Anterior half more flattened; ventral side concave; cytostome in the anterior third; yellowish and granulated; 30 – 50μ long; sapropelic in fresh and brackish water.

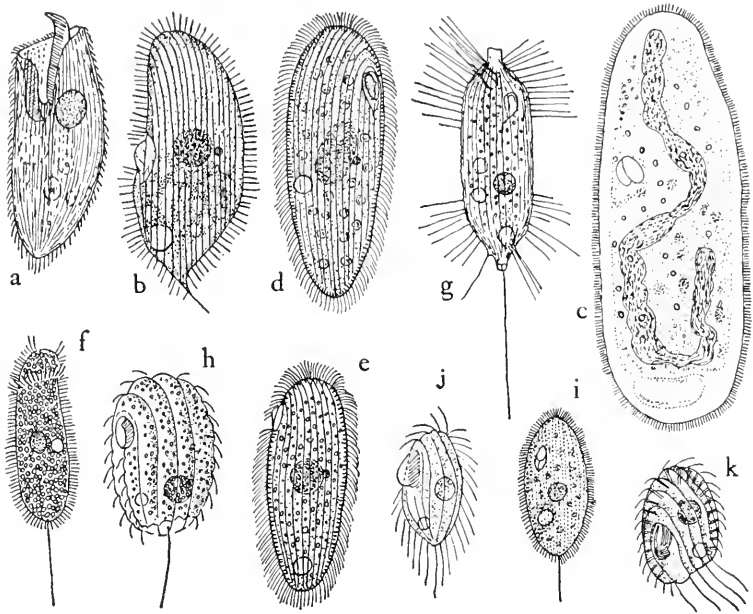


FIG. 251. a, *Espejoia musicola*, $\times 300$ (Penard); b, *Cryptochilidium echini*, $\times 380$ (Powers); c, *Eurychilum actinae*, $\times 360$ (André); d, *Monochilum frontatum*, $\times 440$ (Schewiakoff); e, *Dichilum cuneiforme*, $\times 700$ (Schewiakoff); f, *Loroxcephalus plagius*, $\times 380$ (Stokes); g, *Balanonema biceps*, $\times 600$ (Penard); h, *Platynematum sociale*, $\times 500$ (Kahl); i, *Saprophilus agilitus*, $\times 450$ (Stokes); j, *S. muscorum*, $\times 440$ (Kahl); k, *Cinetochilum margaritaceum*, $\times 440$ (Kahl).

Genus **Saprophilus** Stokes. Ovoid or pyriform; compressed; cytostome in anterior $1/4$ – $1/3$ near right edge; with 2 outer membranes; macronucleus spherical; contractile vacuole posterior; in fresh water.

S. agilitus S. (Fig. 251, i). Ellipsoid; ends bluntly pointed; compressed; plastic; close striation; about 40μ long; in fresh water in decomposing animal matter such as Gammarus.

S. muscorum Kahl (Fig. 251, j). Cytostome large, with a large membrane; trichocysts; contractile vacuole with a distinct canal; body about 35μ long; in fresh water.

Genus **Cinetochilum** Perty. Oval to ellipsoid; highly flattened; cilia on flat ventral surface only; cytostome right of median line in posterior half, with a membrane on both edges, which forms a pocket; oblique non-ciliated postoral field leads to left posterior

end; with 3-4 caudal cilia; macronucleus spherical, central; contractile vacuole terminal; in fresh or salt water.

C. margaritaceum P. (Fig. 251, *k*). 15-45 μ long; in fresh and brackish water.

Genus **Dexiotrichides** Kahl (*Dexiotricha* Stokes). Reniform; compressed; cytostome near middle, with 2 membranes; long cilia sparse; a special oblique row of cilia; a single caudal seta; contractile vacuole terminal; spheroidal macronucleus anterior; a micronucleus; in fresh water. One species.

D. centralis (Stokes) (Fig. 252, *a*). About 30-45 μ long; in decaying vegetable matter.

Genus **Cyrtolophosis** Stokes. Ovoid or ellipsoid; with a mucilaginous envelope in which it lives, but from which it emerges at will; cytostome near anterior end with pocket-forming membrane; on right side a short row of special stiff cilia, bent ventrally; sparse ciliation spiral to posterior-left; spherical macronucleus central; a contractile vacuole; in fresh water.

C. mucicola S. (Fig. 252, *b*). 25-28 μ long; in infusion of leaves.

Genus **Urocentrum** Nitzsch. Short cocoon-shaped, constricted behind the middle; ventral surface flat; 2 broad girdles of cilia; fused cilia at posterior end; with a zone of short cilia in the constricted area; cytopharynx directed toward left, with a stiff ectoplasmic membrane which separates 2 undulating membranes (on left) and ciliated zone (on right); macronucleus, horseshoe-shape, posterior; a micronucleus; contractile vacuole terminal, with 8 long canals which reach the middle of body; in fresh water.

U. turbo (Müller) (Fig. 252, *c*). 50-80 μ long; Kidder and Diller (1934) studied its fission.

Genus **Urozona** Schewiakoff. Ovoid, both ends broadly rounded; a distinct constriction in middle where occur cilia; this ciliary band composed of 5-6 rows of cilia, directed anteriorly and arranged longitudinally; cytostome with a membrane; rounded macronucleus and a micronucleus posterior; contractile vacuole subterminal; in fresh water.

U. butschlii S. (Fig. 252, *d*). 20-25 μ long (Kahl); 30-40 μ (Schewiakoff); in stagnant water.

Genus **Uronema** Dujardin (*Cryptochilum* Maupas). Oval to elongate ovoid; slightly flattened; anterior region not ciliated; inconspicuous peristome with ciliated right edge; cytostome on the ventral side close to left border in the anterior half, with a

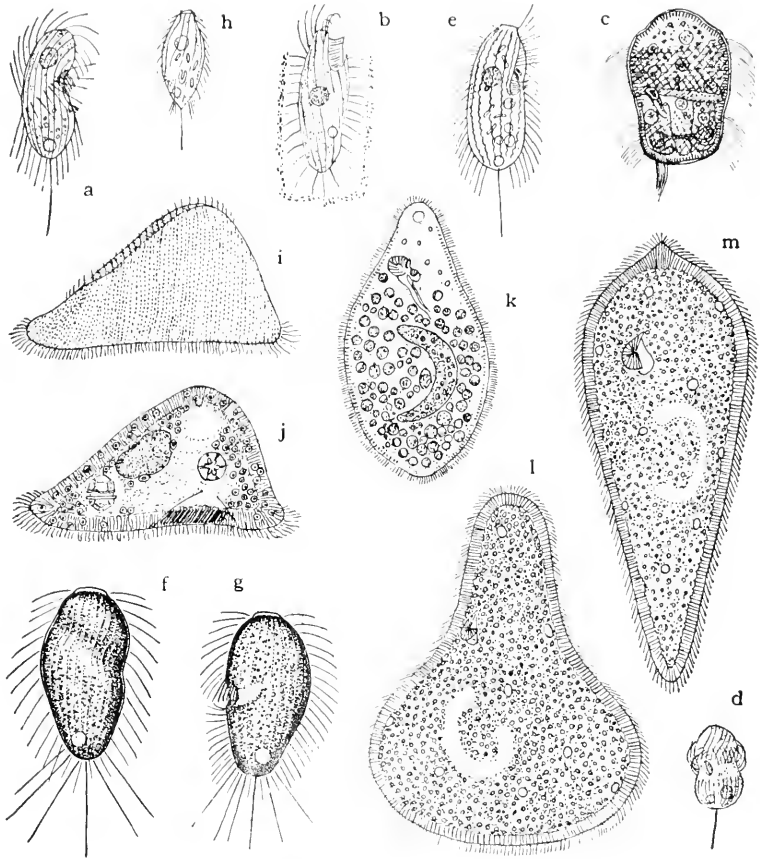


FIG. 252. a, *Dextotrichides centralis*, $\times 500$ (Kahl); b, *Cyrtolophosis mucicola*, $\times 670$ (Kahl); c, *Urocentrum turbo*, $\times 200$ (Bütschli); d, *Urozona butschlii*, $\times 440$ (Kahl); e, *Uronema marina*, $\times 490$ (Kahl); f, g, *U. pluricaudatum*, $\times 940$ (Noland); h, *Homalogastra setosa*, $\times 450$ (Kahl); i, j, *Stokesia vernalis*, $\times 340$ (Wenrich); k, *Ophryoglena collini*, $\times 150$ (Lichtenstein); l, *O. pyriformis*, $\times 180$ (Rossolimo); m, *O. intestinalis*, $\times 55$ (Rossolimo).

small tongue-like membrane; cytopharynx indistinct; macronucleus spherical, central; contractile vacuole terminal; in salt or fresh water.

U. marina D. (Fig. 252, e). 30–50 μ long; in salt water in decaying algae.

U. pluricaudatum Noland (Fig. 252, f, g). Body appears to be

twisted in dorsal view, due to a spiral depression that runs obliquely down toward cytostome; with about 8 caudal setae; in salt water; Florida.

Genus **Homalogastra** Kahl. Broad fusiform; furrows spiral to left; a long caudal seta; a group of cilia on right and left sides of it; macronucleus spherical, anterior; contractile vacuole posterior; in fresh water.

H. setosa K. (Fig. 252, *h*). About 30μ long; fresh water.

Genus **Stokesia** Wenrich. Oblique cone with rounded angles; flat anterior surface uniformly ciliated; with peristome bearing zones of longer cilia, at the bottom of which is located the cytostome; a girdle of longer cilia around the organism in the region of its greatest diameter; pellicle finely striated; with zoochlorellae; trichocysts; free-swimming; in freshwater pond. One species.

S. vernalis W. (Fig. 252, *i, j*). $100\text{--}160\mu$ in diameter; macronucleus; 2–4 micronuclei; fresh water.

Family 2 Ophryoglenidae Kent

Genus **Ophryoglena** Ehrenberg. Ellipsoidal to cylindrical; ends rounded or attenuated; preoral depression in form of '6' due to an ectoplasmic membrane extending from the left edge, cilia on the right edge; cytostome deep-seated; 1 (or 2) contractile vacuole with long radiating canals, opens through pores on right ventral side; macronucleus of various forms with several endosomes; a micronucleus; fresh or salt water or parasitic. Many species.

O. collini Lichtenstein (Fig. 252, *k*). Pyriform; macronucleus horseshoe-shape; $200\text{--}300\mu$ by $120\text{--}230\mu$; in the caecum of *Baetis* larvae.

O. parasitica André. Ovoid; dark; micronucleus (?); $170\text{--}350\mu$ by $180\text{--}200\mu$; in 'intestine' of *Dendrocoelum lacteum*.

O. pyriformis Rossolimo (Fig. 252, *l*). Flask-shape; $240\text{--}300\mu$ long; in intestinal caeca of various Turbellaria.

O. intestinalis R. (Fig. 252, *m*). Up to 1.5 mm. by $450\text{--}500\mu$; smallest 60μ long; in the main intestinal canal of *Dicotylus* sp.

Family 3 Pleuronematidae Kent

Genus **Pleuronema** Dujardin. Ovoid to ellipsoid; peristome begins at anterior end and extends for $2/3$ the body length; a conspicuous membrane at both edges; semicircular swelling to left near oral area; no cytopharynx; close striation longitudinal; 1 to

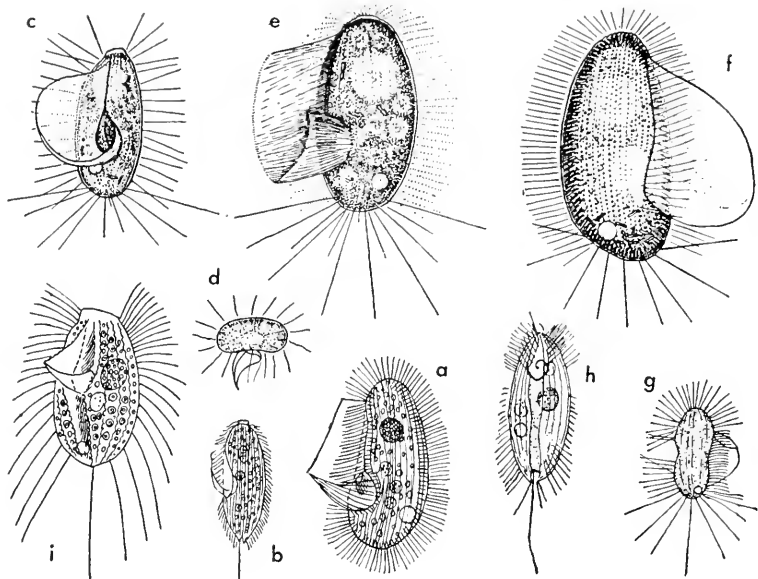


FIG. 253. a, *Pleuronema crassum*, $\times 240$ (Kahl); b, *P. anodontae*, $\times 290$ (Kahl); c, d, *P. setigerum*, $\times 540$ (Noland); e, *P. coronatum*, $\times 540$ (Noland); f, *P. marinum*, $\times 400$ (Noland); g, *Cyclidium litomesum*, $\times 300$ (Stokes); h, *Cristigera phoenix*, $\times 500$ (Penard); i, *C. media*, $\times 400$ (Kahl).

many posterior sensory bristles; macronucleus round or oval; a micronucleus; a contractile vacuole; trichocysts in some species; fresh or salt water, also commensal in freshwater mussels.

P. crassum D. (Fig. 253, a). 70–120 μ long; somewhat compressed; Woods Hole (Calkins).

P. anodontae Kahl (Fig. 253, b). About 55 μ long; posterior bristle about 1/2 the body length; in Sphaerium, Anodonta.

P. setigerum Calkins (Fig. 253, c, d). Ellipsoid; flattened; ventral surface slightly concave; about 25 ciliary rows; 38–50 μ long (Noland); in salt water; Massachusetts, Florida.

P. coronatum Kent (Fig. 253, e). Elongate ovoid; both ends equally rounded; caudal setae long; about 40 ciliary rows; 47–75 μ long (Noland); in fresh and salt water; Florida.

P. marinum D. (Fig. 253, f). Elongate ovoid; trichocysts distinct; caudal setae medium long; about 50 ciliary rows; 51–126 μ long (Noland); in salt water; Florida.

Genus **Cyclidium** Müller. Small ($15\text{--}60\mu$ long); ovoid; usually with refractile pellicle; with a caudal bristle; peristome near right side; on its right edge occurs a membrane which forms a pocket around cytostomal groove and on its left edge either free cilia or a membrane which unites with that on right; no semicircular swelling on left of oral region; round macronucleus with a micronucleus; contractile vacuole posterior; fresh or salt water. Numerous species.

C. litomesum Stokes (Fig. 253, *g*). About 40μ long; dorsal surface slightly convex with a depression in middle; ventral surface more or less concave; cilia long; in fresh water.

Genus **Cristigera** Roux. Similar to *Cyclidium*; much compressed; with a postoral depression; peristome closer to mid-ventral line; fresh or salt water. Several species.

C. phoenix Penard (Fig. 253, *h*). $37\text{--}45\mu$ long; fresh water.

C. media Kahl (Fig. 253, *i*). $45\text{--}50\mu$ long; in salt water.

Genus **Ctedoctema** Stokes. Similar to *Cyclidium* in body form; peristome nearer median line, diagonally right to left; right peristomal ridge with a sail-like membrane which surrounds the cytostome at its posterior end; trichocysts throughout; fresh water.

C. acanthocrypta S. (Fig. 254, *a*). Ovoid; anterior end truncate; macronucleus round, anterior; about 35μ long; in fresh water among vegetation.

Genus **Calypotricha** Phillips. Somewhat resembles *Pleuronema* or *Cyclidium*; but dwelling in a lorica which is opened at both ends; with zoochlorellae; fresh water.

C. pleuronemoides P. (Fig. 254, *b*). Lorica about 85μ high; body about 50μ long; Kellicott's (1885) form is more elongated; in fresh water.

Genus **Histiobalantium** Stokes. Ovoid; ventral side flattened; ciliation uniform; long stiff cilia distributed over the entire body surface; peristome deep; both anterior and posterior regions with a well-developed membrane, connected with the undulating membrane; macronucleus in 2 parts; 1–2 micronuclei; several contractile vacuoles distributed; fresh water.

H. natans (Claparède et Lachmann) (Fig. 254, *c*). $70\text{--}110\mu$ long.

H. semisetatum Noland (Fig. 254, *d*). Elongate ellipsoid; posterior end bluntly rounded; macronucleus spherical; longer setae on posterior half only; contractile vacuoles on dorsal side; $126\text{--}205\mu$ long; salt water; Florida.

Genus **Pleurocoptes** Wallengren. Ovoid, dorsal side hemispherical, ventral side flattened; peristome large, reaching the posterior 1/3; cytopharynx indistinct; longer cilia along peristome; macronucleus spherical; several micronuclei; contractile vacuole terminal; ectocommensal.

P. hydractinae W. (Fig. 254, e). 60–70 μ long; on *Hydractinia echinata*.

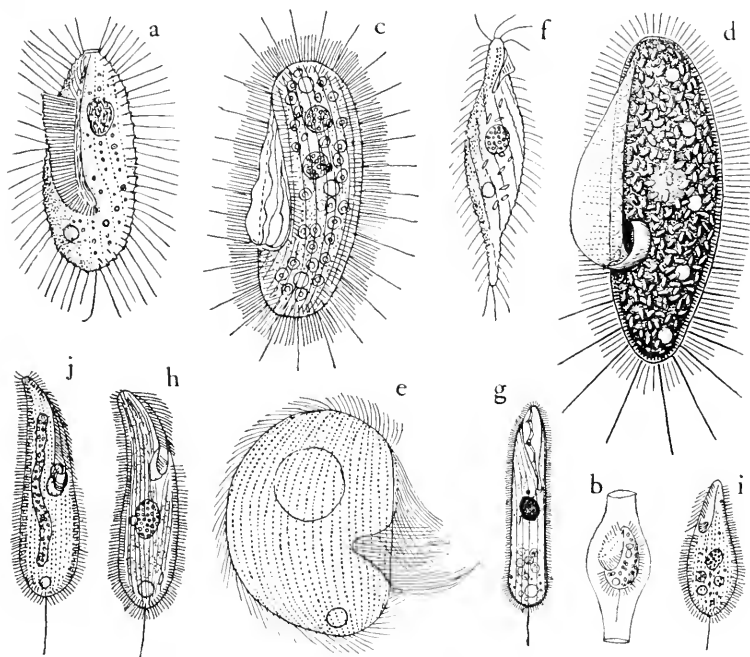


FIG. 254. a, *Ctedoctema acanthocrypta*, $\times 840$ (Kahl); b, *Calyptotricha pleuronemoides*, $\times 180$ (Kahl); c, *Histiobalantium natans*, $\times 420$ (Kahl); d, *H. semisetatum*, $\times 270$ (Noland); e, *Pleurocoptes hydractinae*, $\times 470$ (Wallengren); f, *Cohnilembus fusiformis*, $\times 560$ (Kahl); g, *C. caeci*, $\times 390$ (Powers); h, *Philaster digitiformis*, $\times 220$ (Kahl); i, *P. armata*, $\times 240$ (Kahl); j, *Helicostoma buddenbrocki*, $\times 190$ (Kahl).

Family 4 **Cohnilembidae** Kahl

Genus **Cohnilembus** Kahl (*Lembus* Cohn). Slender spindle-form; flexible; peristome from anterior end to middle of body or longer, curved to right, with 2 membranes on right edge; a caudal seta or a few longer cilia at posterior end; macronucleus oval, near middle; in salt or fresh water, some endozoic.

C. fusiformis (C.) (Fig. 254, *f*). Striation spiral; peristome about 1/6 the body length; a few cilia at posterior end; oval macronucleus central; contractile vacuole posterior; about 60 μ long; in fresh water.

C. caeci Powers (Fig. 254, *g*). About 32–92 μ long; in intestine of *Tripneustes esculentus* and other echinoids; Tortugas.

Family 5 **Philasteridae** Kahl

Genus **Philaster** Fabre-Domergue (*Philasterides* Kahl). Body cylindrical; peristome about 1/3–2/5 the body length, broader near cytostome and with a series of longer cilia; cytostome with a triangular membrane; cytopharynx (?); ciliation uniform; a caudal seta; trichocysts; oval macronucleus with a micronucleus in middle; contractile vacuole terminal or central; in salt or fresh water.

P. digitiformis F.-D. (Fig. 254, *h*). Anterior region bent dorsally; contractile vacuole terminal; 100–150 μ long; salt water.

P. armata (K.) (Fig. 254, *i*). Anterior end more or less straight; peristome difficult to see; contractile vacuole central; 70–80 μ long; fresh water.

Genus **Helicostoma** Cohn. Similar to *Philaster* in general appearance; preoral side-pouch curved around posterior edge of peristome and separated from it by a refractile curved band; with or without pigment spot near cytostome; macronucleus oval or band-form; contractile vacuole terminal; in salt water.

H. buddenbrocki Kahl (Fig. 254, *j*). 130–200 μ long; in salt and brackish water.

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CHAPTER 35

Order 1 **Holotricha** Stein (continued)

Suborder 5 **Thigmotricha** Chatton et Lwoff

THE majority of the ciliates placed in this suborder inhabit the mantle cavity of mussels. They possess thigmotactic cilia with which they attach themselves to the host body. Though appearing heterogeneous, Chatton and Lwoff hold that there is a phylogenetic unity among them, which has been brought about by the degenerative influence because of the similar conditions of habitat.

Without tentacles

Ciliation uniform; ciliary rows meridional, close; peristome does not begin near the anterior end

Thigmotactic cilia on entire broad side; with large peristome. Family 1 Conchophthiridae

Thigmotactic cilia only on a small field of left broad side; peristome small. Family 2 Thigmophryidae (p. 561)

Ciliation unequal on 2 broad sides or spirally arranged, or greatly rudimentary

Cytostome with conspicuous peristome bearing long cilia. Family 3 Ancistrumidae (p. 562)

Cytostome rudimentary. Family 4 Sphenophryidae (p. 565)

With tentacular attaching organella. Family 5 Hypocomidae (p. 566)

Family 1 **Conchophthiridae** Reichenow

Genus **Conchophthirus** Stein. Oval to ellipsoid; flattened; right margin concave at cytostomal region, left margin convex; ventral surface somewhat flattened, dorsal surface convex; cytostome on right side near middle in a depression with an undulating membrane; macronucleus; micronucleus; contractile vacuole opens through a canal to right side; in mantle cavity and gills of various mussels. Kidder made careful studies of several species.

C. anodontae (Ehrenberg) (Figs. 60; 255, *a*). Ovoid; cytostome on dorsal surface in anterior third, with an overhanging projection in front; cytopharynx, surrounded by circular fibrils, continues down as a fine, distensible tubule, to behind the macronucleus; with peristomal basket; ciliary grooves originate in a wide ventral suture near anterior end; anterior region filled with re-

fractile granules; macronucleus posterior; contractile vacuole between nuclei and peristome, with a slit-like aperture (Fig. 27); $65\text{--}125\mu$ by $47\text{--}86\mu$; in mantle cavity, gills and on non-ciliated surface of palps of *Elliptio complanatus*; Woods Hole.

C. curtus Engelmann. Somewhat broader; $60\text{--}125\mu$ by $50\text{--}90\mu$; peristomal field smaller; cytopharynx less conspicuous, but longer; ciliation dense; endoplasmic granules are more closely packed and do not extend as far out toward anterior end; macronucleus central; Kidder found this ciliate in the mantle cavity of *Anodonta marginata*, *A. implicata*, *A. catarecta*, *Lampsilis radiata*, *L. cariosa* and *Alasmidonta undulata* which were obtained from the freshwater lakes of Massachusetts and New York.

C. magna Kidder. Much larger; $123\text{--}203\mu$ by $63\text{--}116\mu$; closer ciliation; anterior $1/3$ filled with smaller granules; irregularly outlined macronucleus, $25\text{--}30\mu$ in diameter, central; 2 (or 1) micronuclei; aperture for contractile vacuole large; mantle cavity of *Elliptio complanatus*; Massachusetts.

C. caryoclada K. (Fig. 255, b). Oval; extremely flattened; leaf-like; cytostome small, in posterior fourth; macronucleus conspicuously branched; 2 (1) micronuclei; $140\text{--}250\mu$ by $90\text{--}160\mu$; mantle cavity of the edible clam, *Siliqua patula*; Oregon.

C. mytili De Morgan (Fig. 53). Reniform; $130\text{--}202\mu$ by $76\text{--}161\mu$; peristomal groove on right side; trichocysts conspicuous along frontal margin; macronucleus oval; 2 micronuclei. Kidder (1933) found the organism on the foot of the common mussel, *Mytilus edulis*, in New York and studied its division and conjugation.

Genus **Myxophyllum** Raabe. Oval or spheroid; pellicle elastic and flexible; peristome on posterior right, without undulating membrane; 7 macronuclei; a micronucleus; ciliation uniform; in the slime covering land pulmonates.

M. steenstrupi (Stein) (Fig. 255, c). 120μ by $100\text{--}120\mu$; on *Succinea putris*, etc.

Family 2 Thigmophryidae Chatton et Lwoff

Genus **Thigmophrya** Chatton et Lwoff. Elongate; round or oblong in cross-section; cytostome in posterior third; contractile vacuole opens in cytopharynx; on gills or palps of lamellibranchs.

T. macomae C. et L. Elongate ovoid; flattened; ventral surface slightly concave; oral funnel opened; contractile vacuole opens at

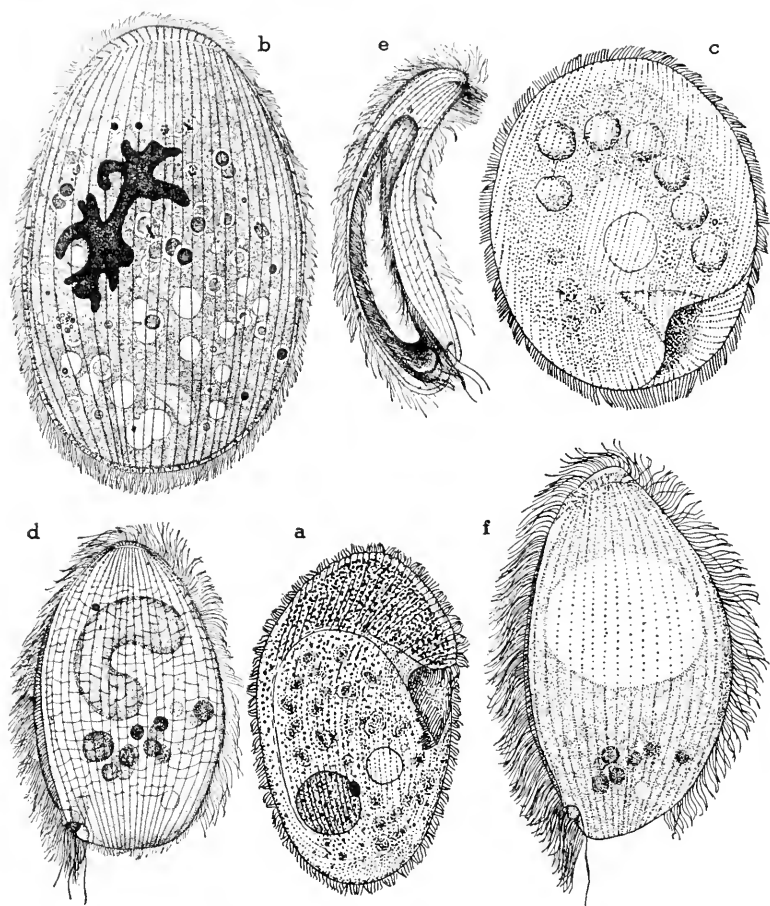


FIG. 255. a, *Conchophthirus anodontae*, $\times 400$ (Kidder); b, *C. caryoclada*, $\times 270$ (Kidder); c, *Myxophyllum steenstrupi*, $\times 370$ (Raabe); d, e, *Ancistruma mytili*, $\times 670$ (Kidder); f, *A. isseli*, $\times 670$ (Kidder).

the bottom of cytopharynx; numerous ciliary rows; about 110μ by 40μ ; on gills of *Macoma* (*Tellina*) *balthica*.

Family 3 **Ancistrumidae** Issel

Genus **Ancistruma** Strand (*Ancistrum* Maupas). Ovoid, pyriform or somewhat irregular; flattened; right side with more numerous large cilia than the left; peristome on right side; cyto-

stome near posterior extremity; macronucleus round or sausage-shape, central; a micronucleus; contractile vacuole posterior; commensal in mantle cavity of various marine mussels. Many species.

A. mytili (Quennerstedt) (Figs. 18; 255, *d, e*). Oval; dorsal surface convex, ventral surface concave; dorsal edge of peristome curves around the cytostome; peristomal floor folded and protruding; longitudinal ciliary rows on both surfaces; 3 rows of long cilia on peristomal edges; macronucleus sausage-form; a compact micronucleus anterior; $52\text{--}74\mu$ by $20\text{--}38\mu$; Kidder (1933) found it in abundance in the mantle cavity of *Mytilus edulis* at Woods Hole and New York.

A. isseli Kahl (Fig. 255, *f*). Pointed at both ends; $70\text{--}88\mu$ by $31\text{--}54\mu$; Kidder (1933) observed it abundantly in mantle cavity of the solitary mussel, *Modiola modiolus*, Massachusetts and New York, and made clear its conjugation and nuclear reorganization.

Genus **Eupoterion** MacLennon et Connell. Small ovoid; slightly compressed; cilia short, in longitudinal rows; rows of long cilia in peristome on mid-ventral surface and extends posteriorly, making a half turn to left around cytostome; small conical cytostome lies in postero-ventral margin of body; contractile vacuole terminal; large round macronucleus anterior; a micronucleus; commensal.

E. pernix M. et C. (Fig. 156, *a*). $46\text{--}48$ ciliary rows; 6 rows of heavy peristomal cilia; $38\text{--}56\mu$ long; in intestinal contents of the mask limpet, *Acmaea persona*; California.

Genus **Ancistrina** Cheissin. Ovoid; anterior end attenuated; peristomal field along narrow right side; $15\text{--}18$ ciliary rows parallel to peristomal ridges; cytostome right-posterior, marked with oral ring, with a membrane and a zone of membranellae; right ridge of peristome marked by 2 adoral ciliary rows; macronucleus anterior, spheroidal; a micronucleus; commensal.

A. ovata C. (Fig. 256, *b*). $38\text{--}48\mu$ by $15\text{--}20\mu$; in mantle cavity of molluscs: *Benedictia biacalensis*, *B. limneoides* and *Choanophalus* sp.

Genus **Ancistrella** Cheissin. Elongate; ends rounded; ventral surface less convex than dorsal surface; $16\text{--}17$ longitudinal ciliary rows; ciliation uniform, except anterior-dorsal region, bearing bristle-like longer cilia; 2 adoral ciliary rows on right of peristome, curved dorsally behind cytostome; contractile vacuole posterior;

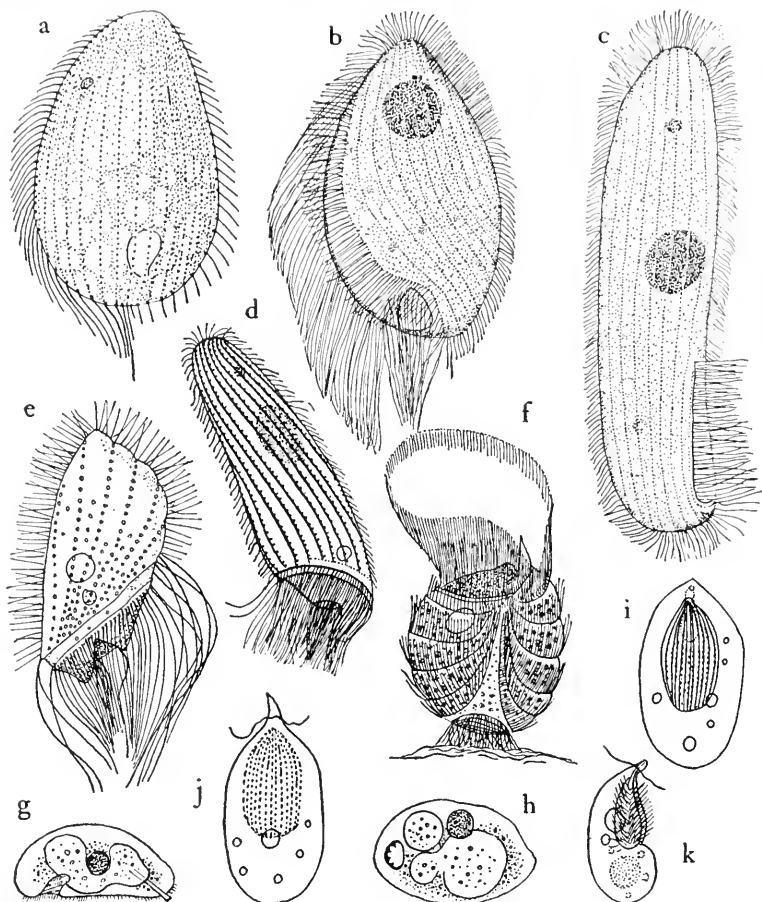


FIG. 256. a, *Eupoterion pernix*, $\times 670$ (MacLennan and Connell); b, *Ancistrina ovata*, $\times 840$ (Cheissin); c, *Ancistrella choanomphali*, $\times 840$ (Cheissin); d, *Boveria teredinidi*, $\times 550$ (Pickard); e, *Plagiospira crinita*, $\times 740$ (Issel); f, *Hemispira asteriasi*, $\times 940$ (Wallengren); g, h, *Hypocoma acinetarum*, $\times 400$ (Collin); i-k, *H. patellarum* (i, j, $\times 820$; k, $\times 670$) (Lichtenstein).

macronucleus single or divided into as many as 7 parts; a micronucleus; commensal.

A. choanomphali C. (Fig. 256, c). $55-90\mu$ by $18-20\mu$; in mantle cavity of *Choanomphalus* sp.

Genus **Ancistrospira** Chatton et Lwoff. Ciliation meridional to spiral; peristome right spiral; commensal.

A. veneris C. et L. 50–60 μ by 22–28 μ ; ovoid; anterior end pointed; ciliary rows meridional; thigmotactic field on left side, sharply marked from body ciliation; on gills of *Venus fasciata*.

Genus **Boveria** Stevens (*Tiarella* Cheissin). Conical; cytostome at posterior end; peristome spiral posteriorly; macronucleus oval, in anterior half; a micronucleus; contractile vacuole posterior; ectocommensal on gills of various marine animals such as *Teredo*, *Bankia*, *Tellina*, *Capsa* and *Holothuria*. Several species.

B. teredinidi Pickard (Fig. 256, *d*). 27–173 μ by 12–31 μ ; on gills on *Teredo navalis*; California.

Genus **Plagiospira** Issel. Conical; anterior end attenuated; peristome runs spirally from middle of body to cytostome, with long cilia; macronucleus oval, anterior; a micronucleus; contractile vacuole near middle of body; somewhat spirally arranged striae widely apart on right side; commensal.

P. crinita I. (Fig. 256, *e*). 32–58 μ by 18–34 μ ; in *Cardita calyculata* and *Loripes lacteus*.

Genus **Hemispeira** Fabre-Domergue. Nearly spherical; flattened; longitudinal non-ciliated furrow on ventral surface, which encircles thigmotactic posterior cilia; 4–5 cross-furrows of cilia; a huge adoral membrane at anterior end; macronucleus, micronucleus large; contractile vacuole, anterior-right; commensal.

H. asteriasi F.-D. (Fig. 256, *f*). 20–30 μ long; ectocommensal on *Asterias gracilis*.

Genus **Hemispeiropsis** König. Oval; body surface not ciliated, except the aboral end which bears 1–2 cross-rows of cilia and thigmotactic cilia; adoral membrane double; macronucleus large, spherical, with an imbedded micronucleus; contractile vacuole central; ectocommensal.

H. comatulac K. About 23–27 μ long, excluding membrane; on *Comatula mediterranea*.

Family 4 Sphenophryidae Chatton et Lwoff

Genus **Sphenophrya** Chatton et Lwoff. Triangular to crescentic; in mature state, basal rows of cilia distinct on a broad side, converging toward middle, from which budding takes place sideways; in gills of mussels.

S. dosinia C. et L. 120 μ by 15–20 μ ; fixed to interfilamental space of gills of *Dosinia exoleta*.

Family 5 **Hypocomidae** Bütschli

Genus **Hypocoma** Gruber. Cilia confined, or reduced, to hold-fast organella at anterior end, arranged in longitudinal rows; with a sucking tentacle which probably serves for obtaining nourishment; cytostome apparently vestigial; commensal. The genus has been placed in Suctoria; but Chatton and Lwoff showed that ciliation is lengthwise and not crosswise as in Suctoria.

H. acinctarum Collin (Fig. 256, *g, h*). On *Acincta papillifera*.

H. patellarum Liechtenstein (Fig. 256, *i-k*). On gills of *Patella caerulea*; about 30 μ long.

H. cardii Chatton et Lwoff. On *Cardium edule*.

Genus **Hypocomides** Chatton et Lwoff. Ovate; slightly flattened; anterior end attenuated, a few meridional striae; adoral rows reduced; commensal in mussels.

H. zyrphaeae C. et L. 25–30 μ by 12–15 μ ; in gills of *Zyrphaea crispata*.

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CHAPTER 36

Order 1 **Holotricha** Stein (continued)

Suborder 6 **Apostomea** Chatton et Lwoff

ASYMMETRICAL forms with a rosette-like cytostome through which liquid or small solid particles are taken into the body; sparse ciliary rows spiral; adoral rows short; macronucleus oval to band-form; a micronucleus; a single contractile vacuole.

The life-cycle of the ciliates grouped here appears to be highly complex and Chatton and Lwoff (1935) distinguished several developmental phases (Fig. 257), as follows: 1) **Trophont** or vegetative phase: right-spiral ciliary rows; nucleus pushed aside by food bodies; body grows, but does not divide. 2) **Protomont**: transitory stage between 1 and 3 in which the organism does not nourish itself, but produces "vitelloid" reserve plates; nucleus central, condensed; ciliary rows become straight. 3) **Tomont**: the body undergoes division usually in encysted condition into more or less a large number of small ciliated individuals. 4) **Protomite**: a stage in which a renewed torsion begins, and which leads to tomite stage. 5) **Tomite**: small free-swimming and non-feeding stage, but serves for distribution. 6) **Phoront**: a stage which is produced by a tomite when it becomes attached to a crustacean and encysts; within the cyst a complete transformation to trophont takes place.

Family **Foettingeriidae** Chatton

Genus **Foettingeria** Caullery et Mesnil. Trophonts large, up to 1 mm. long; sublenticular, anterior end attenuated; dorsal surface convex, ventral surface concave; right side less convex than left side; 9 spiral ciliary rows nearly evenly arranged; in gastro-vascular cavity of various actinozonas; tomont on outer surface of host body, gives rise to numerous tomites with meridional ciliary rows; each tomite becomes a phoront by encysting on a crustacean, and develops into a trophont when taken into gastro-vascular cavity of an actinozoan. One species.

F. actiniarum (Claparède) (Fig. 258, *a*). Phoronts on Copepoda, Ostracoda, Amphipoda, Isopoda and Decapoda; trophonts in

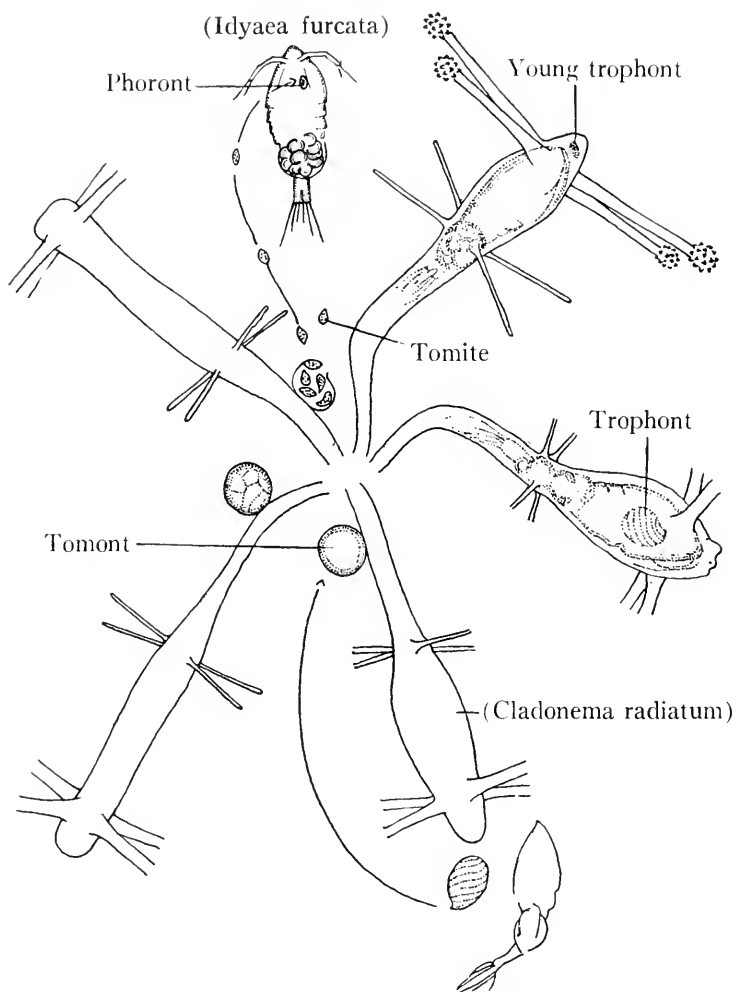


FIG. 257. Diagram illustrating the life-cycle of *Spirophrya subparasitica* (Chatton and Lwoff).

Actinia mesembryanthemum, *A. equina*, *Anemonia sulcata* and other actinozoans in European waters; Chatton and Lwoff found *Metridium marginatum*, *Sagartia leucolena* and *Astrangia danae* of Woods Hole free from this ciliate.

Genus **Spirophrya** Chatton et Lwoff. Trophonts ovoid, pointed anteriorly; 16 uninterrupted ciliary rows of which striae 1 and 2

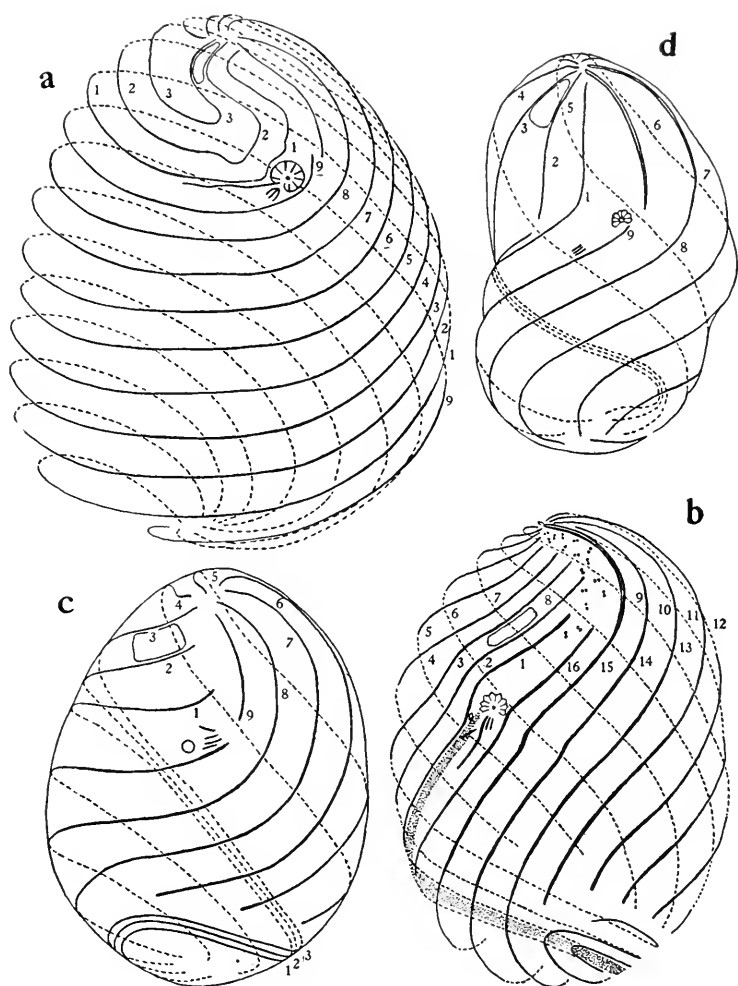


FIG. 258. a, *Foettingeria actiniarum*, a trophont; b, *Spirophrya supparasitica*, a trophont, $\times 1000$; c, *Phoretrophrya nebaliae*, $\times 1180$; d, *Synophrya hypertrophica* (All, Chatton and Lwoff).

approach each other in posterior-dorsal region; phoronts attached to a crustacean; when eaten by *Cladonema*, trophonts enter the crustacean body and complete growth; protomonts upon leaving the host body encyst and each divides into 4–82 tomites (Fig. 257). One species.

S. subparasitica C. et L. (Figs. 257; 258, b). Phoronts attached

to *Idyaca furcata*; ovoid trophonts enter the copepod when eaten by *Cladnema radiatum*.

Genus **Gymnodinioides** Minkiewicz (*Physophaga* Percy; *Oospira* Chatton et Lwoff; *Hyalospira* Miyashita). Trophonts twisted along equatorial plane; generally 9 ciliary rows, in some a rudimentary row between striae 5 and 6 at anterior end. Many species.

G. calkinsi Chatton et Lwoff. Phoronts on gills and trophonts in the moult of *Palaemonetes* sp.; Woods Hole.

Genus **Phoretrophrya** Chatton et Lwoff. Trophonts generally with 9 ciliary rows; striae 1, 2, and 3, close to one another. One species.

P. nebaliae C. et L. (Fig. 258, c). Phoronts and tomonts on appendages, and trophonts in the moult, of *Nebalia geoffroyi*.

Genus **Synophrya** Chatton et Lwoff. Trophonts and tomonts similar to those of *Gymnodinioides*; but development highly complicated. One species.

S. hypertrophica C. et L. (Fig. 258, d). Phoronts in branchial lamellae, and trophonts in the moult, of *Portunus depurator*, etc.

Genus **Ophiurespira** Chatton et Lwoff. Trophonts ovoid; 10 ciliary rows; striae 9 and 10 interrupted. One species.

O. weilli C. et L. (Fig. 259, a). Trophonts in intestine of *Ophiothrix fragilis* and *Amphiura squamata*.

Genus **Photrophrya** Chatton et Lwoff. Trophonts small; ciliation approximately that of *Ophiurespira*; massive macronucleus; with peculiar trichocysts comparable with the nematocysts of *Polykrikos* (p. 228); ecto- or endo-parasitic in encysted stages of other apostomeans. Several species.

P. insidiosa C. et L. (Fig. 259, b). Phoronts, trophonts and tomites in phoronts of *Gymnodinioides*.

Genus **Polyspira** Minkiewicz. Trophonts reniform; 9 rows and several extra rows; striae 1-4 and 5-9 with 2 others in 2 bands.

P. delagei M. (Fig. 260, a). Phoronts on gills and trophonts in the moult of *Eupagurus berhardus*.

Genus **Pericaryon** Chatton. Trophonts ellipsoid; 14 ciliary rows.

P. cesticola C. (Fig. 259, d). Trophonts in gastro-vascular cavity of the ctenophore, *Cestus veneris*; other stages unknown.

Genus **Calospira** Chatton et Lwoff. Trophonts resemble those of *Spirophrya*; 20 ciliary rows; macronucleus twisted band-form; a micronucleus.

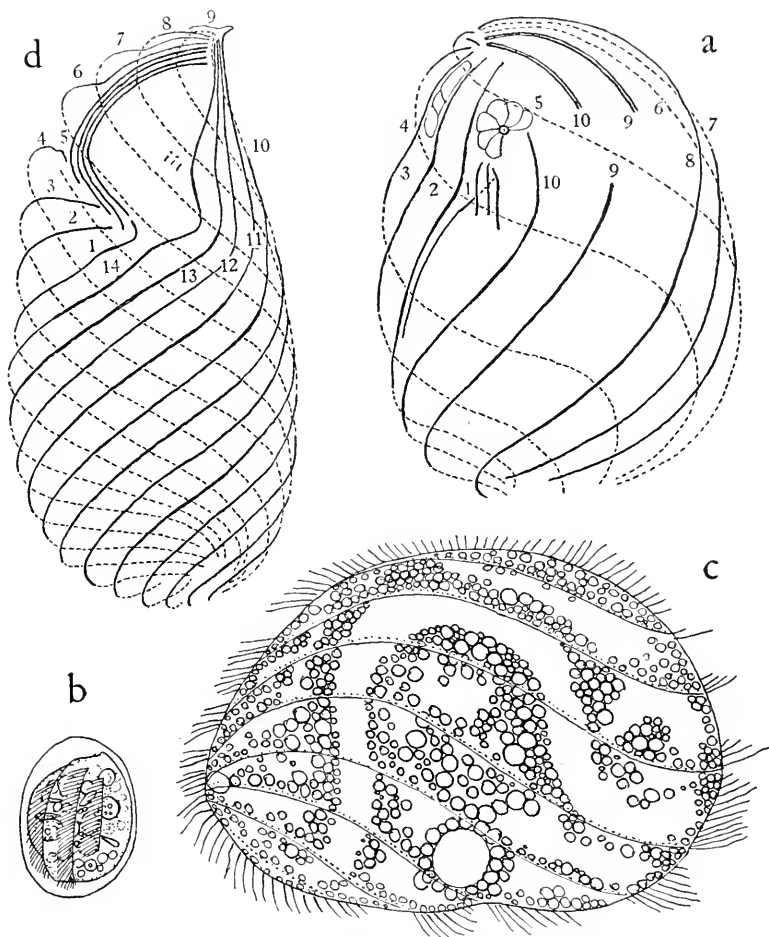


FIG. 259. a, *Ophiurespira weilli*; b, *Photorophrya insidiosa*, a trophont in a phoront of *Gymnoidioides*, $\times 800$; c, *Vampyrophrya pelagica*, a trophont, $\times 740$; d, *Pericaryon cesticola*, a trophont (All, Chatton and Lwoff).

C. minkiewiczii C. et L. (Fig. 260, b). Phoronts attached to integument of *Harpacticus gracilis* (copepod); trophonts in its fresh carcass; tomonts and tomites in water.

Genus **Vampyrophrya** Chatton et Lwoff. Trophonts ovoid; 10 ciliary rows, of which striae 3-8 are uninterrupted. One species.

V. pelagica C. et L. (Fig. 259, c; 260, c). Phoronts on *Paracalanus parvus*, *Clausocalanus furcatus*, etc., and trophonts in their fresh carcasses.

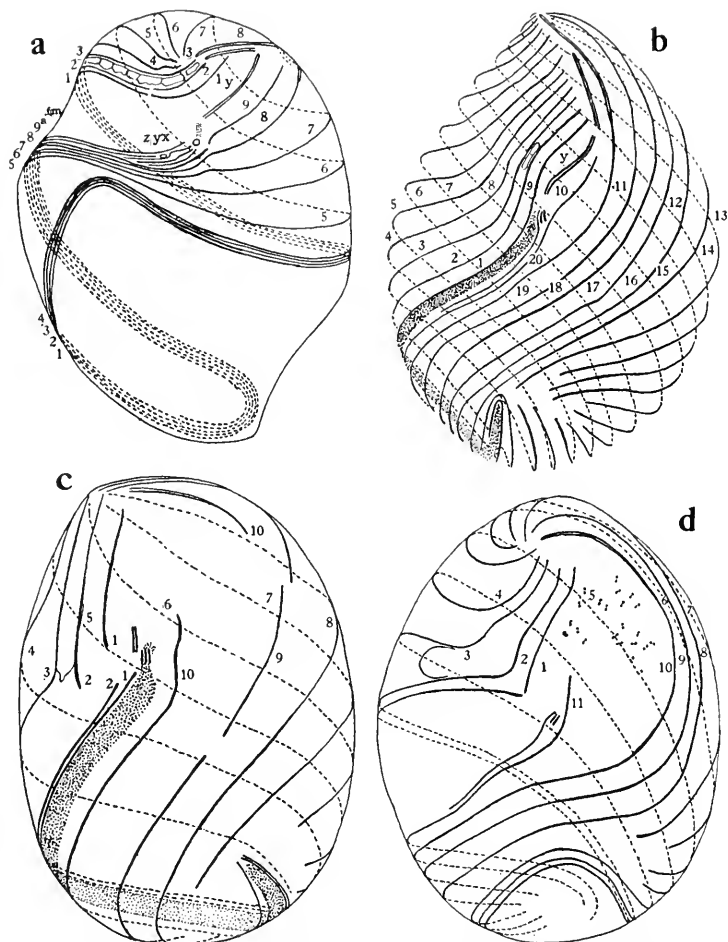


FIG. 260. a, *Polyspira delagei*; b, *Calospira minkiewiczzi*, a trophont, $\times 1300$; c, *Vampyrophrya pelagica*; d, *Traumatophthora punctata*, $\times 1300$ (All, Chatton and Lwoff).

Genus **Traumatophthora** Chatton et Lwoff. Trophonts oval; 11 ciliary rows. One species.

T. punctata C. et L. (Fig. 260, d). Trophonts in fresh carcass of *Acartia clausi*.

Reference

CHATTON, E. and A. LWOFF 1935 Les ciliés apostomes. Arch. zool. exp. et gén., Vol. 77.

CHAPTER 37

Order 2 **Spirotricha** Bütschli

With free cilia only; exceptionally with small groups of cirrus-like projections in addition to cilia

Uniformly ciliated; in Peritromidae dorsal surface without cilia or with a few cilia; in Licnophoridae cilia only on edge of attaching disk; peristome usually extended; peristomal field mostly ciliated.....Suborder 1 Heterotricha

Ciliation much reduced or none at all

Rounded in cross-section; cilia usually much reduced; adoral zone encloses a non-ciliated peristomal field in spiral form.....Suborder 2 Oligotricha (p. 587)

Compressed; carapaced; peristomal zone reduced to 8 membranellae which lie in a oval hollow.....Suborder 3 Ctenostomata (p. 600)

Cirri only, on ventral side; dorsal side usually with rows of short slightly movable bristles.....Suborder 4 Hypotricha (p. 603)

Suborder 1 **Heterotricha** Stein

Body ciliation complete and uniformly the same

Peristome sunk in a funnel-like hollow at anterior end, thus mostly covered.....Family 1 Bursariidae (p. 574)

Peristome lies almost completely free, leading to a short and narrow oral funnel (absent in one family)

A narrow non-ciliated zone on right of adoral zone; usually an undulating membrane or ciliary row to right of this non-ciliated zone and anterior to cytostome; a small peristomal field between the membrane and adoral zone

Adoral zone extends diagonally to posterior-right on ventral surface; highly developed forms, with a long zone twisting spirally around body.....Family 2 Metopidae (p. 576)

Adoral zone parallel to body axis on flat ventral surface, turns somewhat to right in front of cytostome; oral funnel distinct; typically an undulating membrane or a double ciliated furrow in front of cytostome.....Family 3 Spirostomidae (p. 578)

Without the non-ciliated zone; a large peristomal field with a half or completely spiral adoral zone

Peristomal field not ciliated; with a large undulating membrane on its right edge.....Family 4 Condyllostomidae (p. 581)

Peristomal field ciliated; without undulating membrane

Peristomal field not drawn out in 2 wings; free-swimming or secretes gelatinous lorica.....Family 5 Stentoridae (p. 581)

- Peristomal field drawn out into 2 wings; with flask-shaped, thin-walled pseudochitinous lorica..... Family 6 Folliculinidae (p. 584)
- Body ciliation either confined to ventral side or lacking
- Free-living; flattened; cilia only on ventral surface; adoral zone surrounds anterior region of ventral surface; cytostome on left edge near middle of body..... Family 7 Peritromidae (p. 584)
- Ectocommensal; extremities discoid; body narrowed; anterior disk surrounded spirally by adoral zone; posterior disk bears membranous cilia..... Family 8 Lienophoridae (p. 586)

Family 1 Bursariidae Perty

Genus **Bursaria** Müller. Ovoid; anterior end truncate, posterior end broadly rounded; dorsal surface convex, ventral surface flattened; deep peristome begins at anterior end and reaches about central part of body, where it gives rise to cytostome and cytopharynx, which is bent to left; lengthwise fold divides peristome into 2 chambers; striation longitudinal; ciliation complete and uniform; macronucleus band-form; many micronuclei; many contractile vacuoles distributed along lateral and posterior borders; cysts with a double envelope; fresh water. One species.

B. truncatella M. (Fig. 261, a). 500–1000 μ long.

Genus **Thylacidium** Schewiakoff. Similar to *Bursaria* in general appearance; but smaller in size; peristome simple in structure without longitudinal fold; with zoochlorellae; fresh water. One species.

T. truncatum S. (Fig. 261, b). 60–100 μ long.

Genus **Bursaridium** Lauterborn. Similar to *Bursaria*; peristome funnel turns to right; fresh water.

B. difficile Kahl (Fig. 261, c). Anterior end truncate, slanting toward right; about 130 μ long.

Genus **Balantidium** Claparède et Lachmann (*Balantidiopsis* Bütschli; *Balantiodoides* Alexeieff). Oval, ellipsoid to subcylindrical; peristome begins at or near anterior end; cytopharynx not well developed; longitudinal ciliation uniform; macronucleus elongated; a micronucleus; contractile vacuole and cytopyge terminal; in gut of vertebrates and invertebrates. Numerous species. Hegner (1934) states that the size and shape of body and macronucleus could be made a satisfactory basis for specific identification.

B. coli (Malmsten) (Fig. 261, d, e). Ovoid or pyriform; 30–150 μ by 25–120 μ ; oblique peristomal depression below anterior tip;

adoral zone distinct; macronucleus sausage-form; 1-2 contractile vacuoles; cytopyge terminal; food vacuoles with red blood corpuscles, leucocytes, etc.; cysts 50-60 μ long; in colon of man, pigs, and chimpanzees. The infection in man is presumably acquired

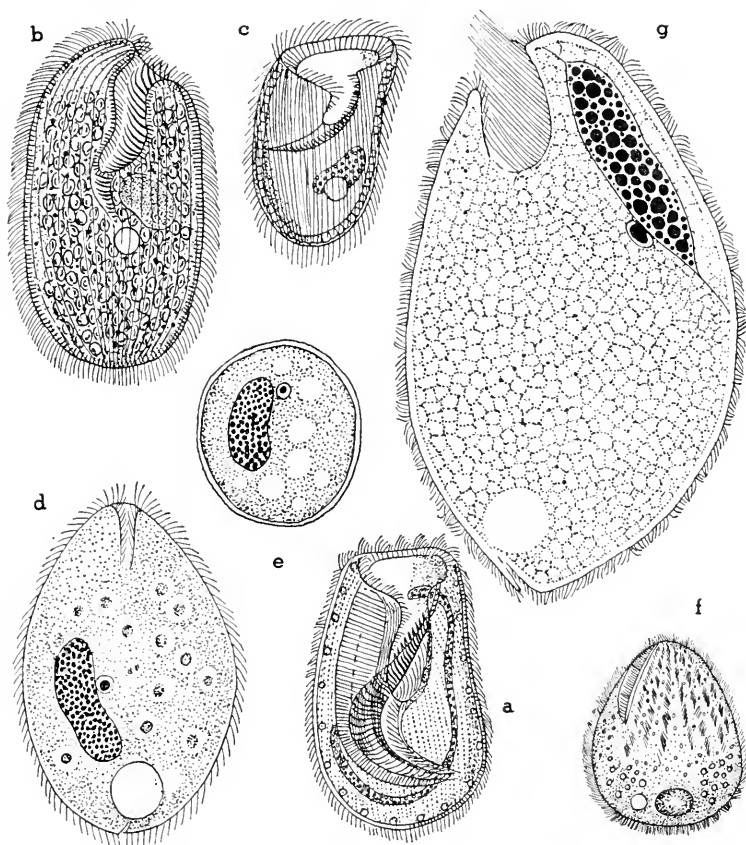


FIG. 261. a, *Bursaria truncatella*, $\times 60$ (Kahl); b, *Thylacidium truncatum*, $\times 440$ (Schewiakoff); c, *Bursaridium difficile*, $\times 210$ (Kahl); d, e, *Balantidium coli*, $\times 540$ (Kudo); f, *B. duodeni*, $\times 170$ (Stein); g, *B. praenucleatum*, $\times 950$ (Kudo and Meglitsch).

through cysts from pigs in which the organism is, as a rule, quite common and is responsible for the balantidiosis in unfortunate patients; widely distributed.

B. suis McDonald. Ellipsoid; 35-120 μ by 20-60 μ ; macronu-

cleus more elongate and narrow; in pigs, apparently not infectious to man.

Other domestic and wild animals harbor various species of *Balantidium*.

B. duodeni Stein (Fig. 261, *f*). 70–80 μ by 55–60 μ ; in intestine of the frog.

B. praenucleatum Kudo et Meglitsch (Fig. 261, *g*). 42–127 μ long, 32–102 μ thick, 25–80 μ wide; macronucleus close to anterior end; in colon of *Blatta orientalis*.

Family 2 Metopidae Kahl

Genus **Metopus** Claparède et Lachmann. Body form changeable because of soft ectoplasm; when extended oblong or fusiform; peristome conspicuous, slightly spirally diagonal, beginning at anterior end and reaching middle of body; when contracted, peristome much spirally coiled; cytopharynx short; body ciliation uniform, longitudinal or in some, spiral; longer cilia at ends; conspicuous contractile vacuole terminal; macronucleus ovoid to elongate; fresh or salt water, some parasitic. Numerous species.

M. es (Müller) (Figs. 76; 262, *a*). 120–200 μ long; sapropelic. Noland's (1927) study on its conjugation has been described (p. 152).

M. striatus McMurich (Fig. 262, *b*). 80–120 μ long; fresh water.

M. fuscus Kahl (Fig. 262, *c*). 180–300 μ long by 60 μ wide and 40 μ thick; fresh water.

M. circumlabens Biggar (Fig. 262, *d*). 70–165 μ by 50–75 μ ; in digestive tract of sea urchins, *Diadema setosum* and *Echinometris subangularis*; Bermuda (Biggar). Powers observed it in *Centrichinus antillarum*, etc., at Tortugas.

Genus **Spirorhynchus** da Cunha. Fusiform; somewhat flattened; anterior end drawn out and curved toward left; posterior end also drawn out; spiral peristome; cytopharynx small with an undulating membrane; cilia uniformly long; contractile vacuole posterior; longitudinally striated; body surface with closely adhering bacteria (Kirby); 3 spherical macronuclei; micronucleus (?); in brackish water.

S. verrucosus d. C. (Fig. 262, *e*). 122–140 μ by 20–22 μ ; Kirby observed it in salt marsh with 3 per cent salinity; California.

Genus **Caenomorphia** Perty (*Gyrocoris* Stein). Bell-shaped; carapaced ectoplasm in some species bears protrichocysts; strong

marginal zone of about 8 rows of cilia; 1–2 dorsal rows of longer cilia and a dense spiral field around caudal prolongation; peristome long; cytostome posterior; cytopharynx directed anteriorly.

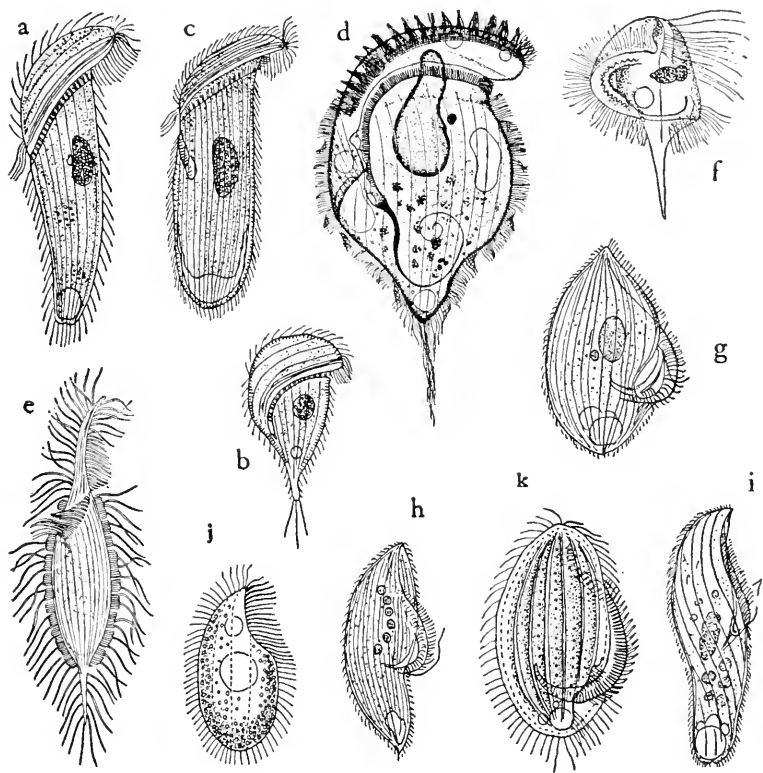


FIG. 262. a, *Metopus es*, $\times 260$ (Kahl); b, *M. striatus*, $\times 220$ (Kahl); c, *M. fuscus*, $\times 150$ (Kahl); d, *M. circumlabens*, $\times 370$ (Powers); e, *Spirotrichus verrucosus*, $\times 360$ (Kirby); f, *Caenomorpha medusula*, $\times 200$ (Blochmann); g, *Blepharisma lateritium*, $\times 160$ (Penard); h, *B. persicinum*, $\times 290$ (Penard); i, *B. steini*, $\times 340$ (Penard); j, *Protocruzia pigerrima*, $\times 390$ (Faria, da Cunha and Pinto); k, *Phacodinium metschnikoffi*, $\times 270$ (Kahl).

only; a single elongate or 2 spherical macronuclei; a micronucleus; fresh or salt water (sapropelic). Several species.

C. medusula P. (Fig. 262, f). 150μ by 130μ ; fresh and brackish water. Several varieties.

Family 3 **Spirostomidae** Kent

Genus **Spirostomum** Ehrenberg. Elongated; cylindrical; somewhat compressed; ectoplasm with highly developed myonemes which are arranged lengthwise independent of ciliary rows, hence highly contractile; yellowish to brown; excretory vacuole terminal large, with a long dorsal canal; macronucleus either ovoid or chain form; cilia short; rows longitudinal; caudal cilia are thigmotactic, secrete mucous threads (Jennings); peristome lined closely with short membranellae; fresh or salt water. Several species.

S. ambiguum E. (Fig. 263, *a*). 1–3 mm. long (length:width, 10:1); macronucleus chain-form; peristome $\frac{2}{3}$ the body length; fresh water.

S. minus Roux (Figs. 36; 263, *b*). 500–800 μ long; macronucleus chain-form; in fresh and salt water (Kahl).

S. loxodes Stokes (Fig. 263, *c*). About 300 μ long (length:width, 6–7:1); peristome about $\frac{1}{3}$ the body length; oblique striation; longer cilia at ends; macronucleus chain-form; fresh water.

S. intermedium Kahl (Fig. 263, *d*). Slender; 400–600 μ long; macronucleus chain-form; fresh water.

S. teres Claparède et Lachmann (Fig. 263, *e*). 150–400 μ long; macronucleus oval; in fresh water and also reported from salt water.

S. filum (E.) (Fig. 263, *f*). Peristome $\frac{1}{4}$ the body length; posterior end drawn out; 200–300 μ up to 700 μ long; fresh water.

Genus **Gruberia** Kahl. Similar to *Spirostomum* in general appearance; but posterior end drawn out; slightly contractile; contractile vacuole posterior; macronucleus compact or beaded; salt water.

G. calkinsi Beltran (Fig. 263, *g*). 200–800 μ long; peristome $\frac{2}{3}$ the body length; many (contractile ?) vacuoles distributed; Woods Hole.

Genus **Blepharisma** Perty. Pyriform, spindle-form or ellipsoid; somewhat narrowed anteriorly; compressed; peristome on left border, which is twisted to right at posterior end and connected with oral funnel with membrane; in front of cytostome a 2-layered undulating membrane on right edge; ciliary rows longitudinal; ciliation dense; contractile vacuole and cytopyge terminal; macronucleus one or divided into several parts; several species rose-colored; fresh or salt water. Many species.

B. lateritium (Ehrenberg) (Fig. 262, *g*). 130–200 μ long; pyri-

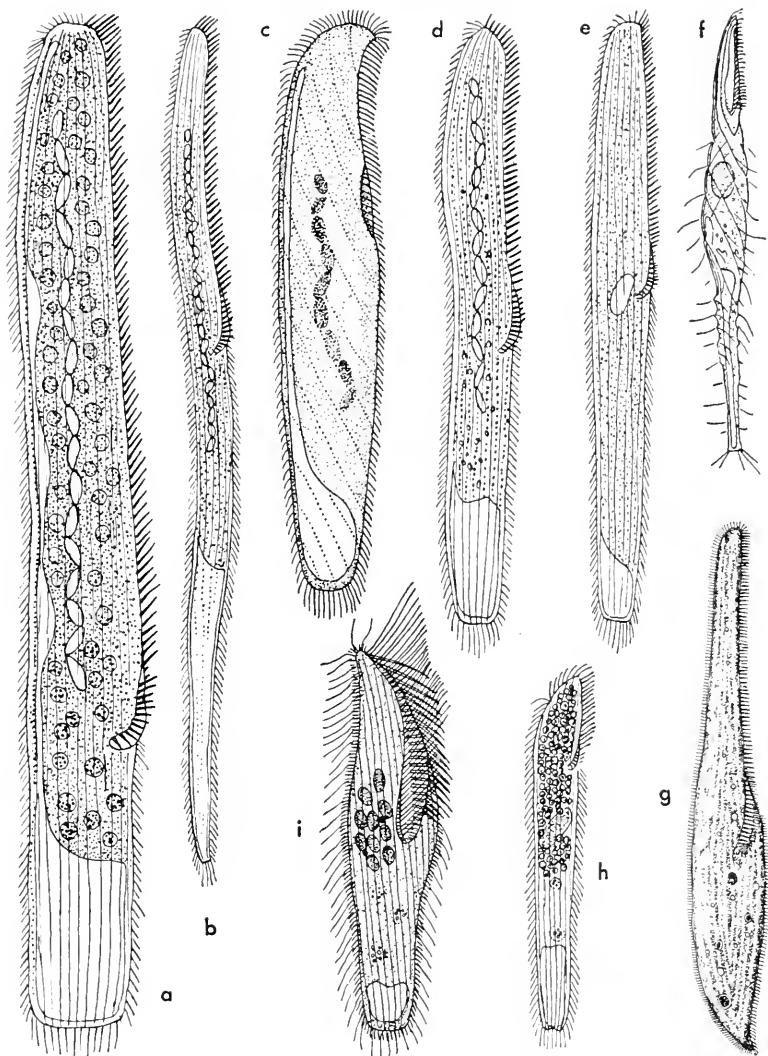


FIG. 263. a, *Spirostomum ambiguum*, $\times 65$ (Kahl); b, *S. minus*, $\times 140$ (Kahl); c, *S. loxodes*, $\times 240$ (Stokes); d, *S. intermedium*, $\times 140$ (Kahl); e, *S. teres*, $\times 200$ (Kahl); f, *S. filum*, $\times 190$ (Penard); g, *Gruberia calkinsi*, $\times 140$ (Bertran); h, *Pseudoblepharisma tenuis*, $\times 310$ (Kahl); i, *Parablepharisma pellitum*, $\times 340$ (Kahl).

form; macronucleus oval; a micronucleus; rose-colored; fresh water among decaying leaves.

B. perisinum P. (Fig. 262, *h*). 80–120 μ long; elongate oval; posterior end pointed; left peristomal edge sigmoid; preoral membrane large; macronucleus in 3–7 parts; rose-colored; fresh water among decaying vegetation.

B. steini Kahl (Fig. 262, *i*). 80–200 μ long; macronucleus ovoid; reddish to colorless; fresh water in sphagnum.

B. undulans Stein. 150–300 μ long; macronucleus in 2 parts; undulating membrane long; cytopharynx directed posteriorly; fresh water among decaying vegetation. Moore (1934) studied its contractile vacuole and Giese (1938) observed the influence of light upon its coloration (p. 37).

Genus **Protocruzia** Faria, da Cunha et Pinto. Peristome does not turn right, leads directly into cytostome; convex left side not ciliated, but bears bristles; flat right side with 3–5 faintly marked ciliary rows; peristome begins at pointed anterior end and extends $1/4$ – $1/3$ the body length; cytopharynx (?); macronucleus simple; contractile vacuole subterminal; salt water.

P. pigerrima (Cohn) (Fig. 262, *j*). About 20 μ (da Cunha); 50–60 μ long (Kahl); peristome $1/4$ – $1/3$ the body length; salt water.

Genus **Phacodinium** Prowazek. Oval; marked grooves on body surface; cilia in cirrus-like fused groups; peristome long on left margin; cytostome posterior; contractile vacuole terminal; macronucleus horseshoe-shape; 5–9 micronuclei; fresh water. One species.

P. metchnikoffi (Certes) (Fig. 262, *k*). About 100 μ long.

Genus **Pseudoblepharisma** Kahl. Body form intermediate between *Spirostomum* and *Blepharisma*; right peristomal edge with 2 rows of cilia; fresh water.

P. tenuis K. (Fig. 263, *h*). 100–200 μ long.

Genus **Parablepharisma** Kahl. Similar to *Blepharisma*; but peristome-bearing anterior half narrowed neck-like and pointed; ectoplasm covered with gelatinous layer in which symbiotic bacteria are imbedded; salt water.

P. pellitum K. (Fig. 263, *i*). 120–180 μ long.

Genus **Nyctotherus** Leidy. Oval or reniform; compressed; peristome begins at anterior end, slightly turns to right and ends in cytostome located midway between the ends; cytopharynx runs dorsally and posteriorly, a long tube with undulating membrane; ciliary rows longitudinal and close-set; massive macronucleus in anterior half with a micronucleus; in some, nuclei are suspended

by karyophore; endoplasm with discoid glycogenous substance, especially in anterior region, hence yellowish to brown; contractile vacuole and cytopyge terminal; in colon of Amphibia and various invertebrates. Numerous species.

N. ovalis L. (Figs. 3; 264, *a*, *b*). Ovoid; anterior half compressed; macronucleus elongate, at right angles to dorso-ventral axis at anterior $1/3$; micronucleus in front of macronucleus; distinct karyophore; glycogen bodies; $90\text{--}185\mu$ by $62\text{--}95\mu$; giant forms up to 360μ by 240μ ; cysts $72\text{--}106\mu$ by $58\text{--}80\mu$; in colon of cockroaches. The chromatin spherules of the macronucleus are often very large (p. 35).

N. cordiformis (Ehrenberg) (Figs. 75; 264, *c*). $60\text{--}200\mu$ by $40\text{--}140\mu$; ovoid; micronucleus behind macronucleus; no karyophore; in colon of frogs and toads. Wichterman (1936) studied its life-cycle in *Hyla versicolor* (Fig. 75).

Family 4 Condylostomidae Kahl

Genus **Condylostoma** Dujardin. Ellipsoid; anterior end truncate, posterior end rounded or bluntly pointed; slightly flattened; peristome wide at anterior end and V-shaped, peristomal field not ciliated; a large membrane on right edge and adoral zone on left; macronucleus moniliform; one to several contractile vacuoles often with canal; cytopyge posterior; fresh or salt water. Many species.

C. vorticella (Ehrenberg) (Fig. 264, *d*). $100\text{--}200\mu$ long; fresh water.

C. patens (Müller). $350\text{--}550\mu$ long; salt water; Woods Hole (Calkins).

Family 5 Stentoridae Carus

Genus **Stentor** Oken. When extended, trumpet-shaped or cylindrical; highly contractile; some with mucilaginous lorica; usually oval to pyriform while swimming; conspicuous peristomal field frontal; adoral zone encircles peristome in a spiral form, leaving a narrow gap on ventral side; the zone and field sink toward cytostome and the former continues into cytopharynx; macronucleus round, oval or elongated, in a single mass or in divided parts; contractile vacuole anterior-left; free-swimming or attached; fresh water.

S. coeruleus Ehrenberg (Figs. 14; 264, *e*). Fully extended body

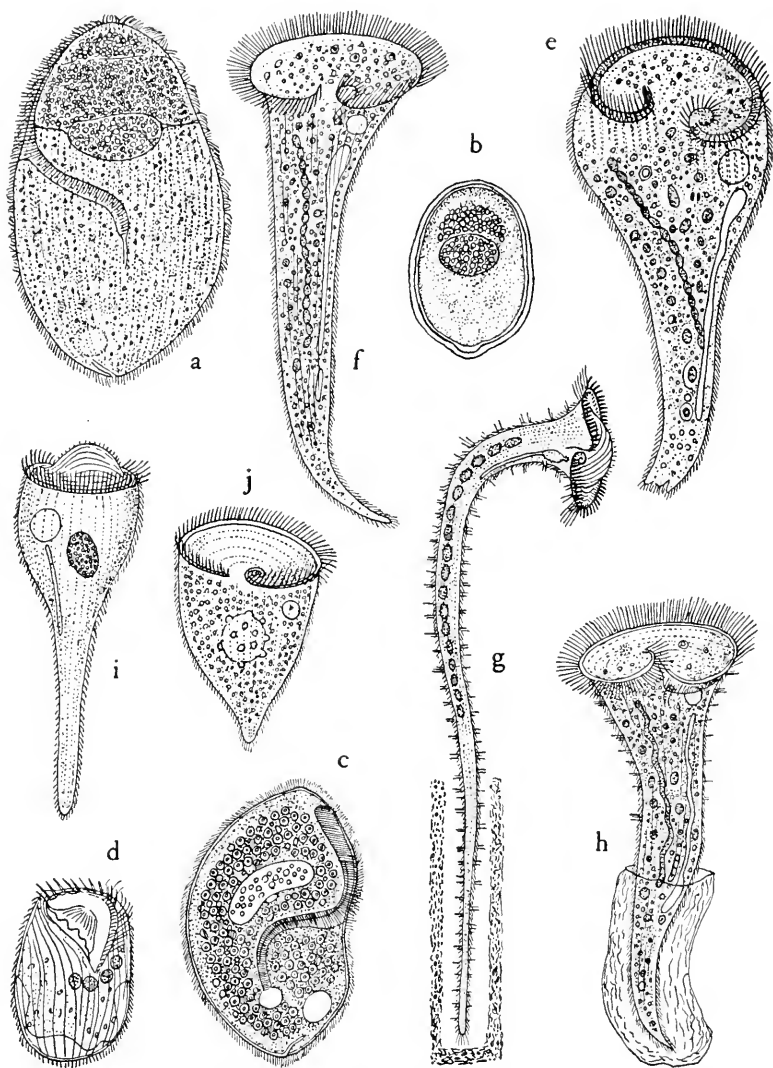


FIG. 264. a, b, *Nyctotherus ovalis*, $\times 340$ (Kudo); c, *N. cordiformis*, $\times 170$ (Stein); d, *Condyllostoma vorticella*, $\times 120$ (Penard); e, *Stentor coeruleus*, somewhat contracted, $\times 70$ (Roux); f, *S. polymorphus*, $\times 60$ (Roux); g, *S. mulleri*, $\times 50$ (Kahl); h, *S. roeseli*, $\times 75$ (Roux); i, *S. igneus*, $\times 160$ (Kahl); j, *S. amethystinus*, $\times 100$ (Kahl).

1–2 mm. long; anterior end greatly expanded; the beautiful blue color is due to a pigment, stentorin, lodged in interstriation granules; macronucleus beaded; Burnside (1929) studied its body and nuclear sizes (p. 114).

S. striatus Barraud-Maskett. Dark bluish green; funnel-shape; peristomal edge irregularly undulating; striation conspicuous; macronucleus beaded; up to 2.2 mm. long.

S. polymorphus (Müller) (Fig. 264, *f*). Colorless; with zoochlorellae; 1–2 mm. long when extended; macronucleus beaded; anterior end expanded.

S. mulleri (Bory) (Fig. 265, *g*). Colorless; with zoochlorellae; 2–3 mm. long; anterior end expanded; posterior portion drawn out into stalk, often housed in a gelatinous tube; on body surface 3–4 longer and stiff cilia grouped among cilia; macronucleus moniliform.

S. roeseli Ehrenberg (Fig. 264, *h*). 0.5–1 mm. long; anterior end expanded; body surface with groups of longer cilia; posterior portion, drawn out and often housed in a gelatinous tube; macronucleus long band-form.

S. igneus E. (Fig. 264, *i*). Rose-colored or colorless; 200–400 μ long; macronucleus oval; ciliation uniform.

S. niger (Müller). Yellowish or brown; macronucleus oval; 200–300 μ long.

S. multiformis (Müller). Dark blue to bluish green; anterior end not expanded; 150–200 μ long; macronucleus oval.

S. amethystinus Leidy (Fig. 264, *j*). Habitually pyriform (contracted); amethyst-blue; with zoochlorellae; 300–600 μ long; macronucleus oval.

S. pyriformis Johnson. When extended 500 μ long; anterior end 200 μ in diameter.

Genus **Fabrea** Henneguy. Pyriform; posterior end broadly rounded, anterior end bluntly pointed; peristome extends down from anterior end $\frac{2}{5}$ or more the body length, its posterior portion closely wound; peculiar black spot beneath membranellae in anterior portion of spiral adoral zone, composed of numerous pigment granules; without contractile vacuole; macronucleus, a sausage-shaped body or in 4 parts; in salt water.

F. salina H. (Fig. 265, *a*, *b*). 120–220 μ by 67–125 μ (Kirby); 130–450 μ by 70–200 μ (Henneguy); cysts ovoidal, with gelatinous envelope; 89–111 μ by 72–105 μ . Kirby (1934) found the organism

in ditches and pools in salt marshes, showing salinities 7.5–20.1 per cent in California.

Genus **Climacostomum** Stein. Oval; flattened; right edge of peristome without membrane, left edge, semicircular or spiral with a strong adoral zone; peristomal field ciliated; cytopharynx long curved tube with a longitudinal row of cilia; macronucleus band-form; contractile vacuole terminal, with 2 long canals; fresh or brackish water.

C. virens Ehrenberg (Fig. 265, *c*). 100–300 μ long; with or without zoochlorellae; fresh and brackish water.

Family 6 Folliculinidae Dons

Genus **Folliculina** Lamarck. Lorica attached on broad surface; neck oblique to perpendicular; sometimes with collar or spiral ridge; neck uniform in diameter; salt water.

F. moebiusi Kahl. (Fig. 265, *d*). Lorica about 500 μ high.

F. producta (Wright) (Fig. 265, *e*). Lorica yellowish brown; 250 μ long; neck often long; Atlantic coast.

Genus **Microfolliculina** Dons. Posterior end or sides of lorica with sack-like protuberances.

M. limnoriae (Giard). Lorica dark blue; pellicle faintly striated; salt water.

Genus **Pseudofolliculina** Dons. Lorica attached with posterior end; more or less vertical; without ring-furrow in middle; with or without style; salt water.

P. arctica D. (Fig. 265, *f*). Lorica about 430 μ high, with spiral ridge; off Norwegian coast 15–28 m. deep.

Genus **Parafolliculina** Dons. Neck of lorica with a basal swelling; attached either with posterior end or on a lateral surface; salt water.

P. violacea (Giard) (Fig. 265, *g*). 200–300 μ long; salt water.

Family 7 Peritromidae Stein

Genus **Peritromus** Stein. Ovoid; ventral surface flattened, dorsal surface with hump of irregular outline bearing a few dorsal setae; ciliary rows only on ventral surface; a small undulating membrane at posterior end of peristome; short marginal spines; 2 macro- and 2 micro-nuclei; salt water.

P. californicus Kirby (Fig. 265, *h*). Peristome short; left margin slightly concave; dorsal hump with wart-like protuberances,

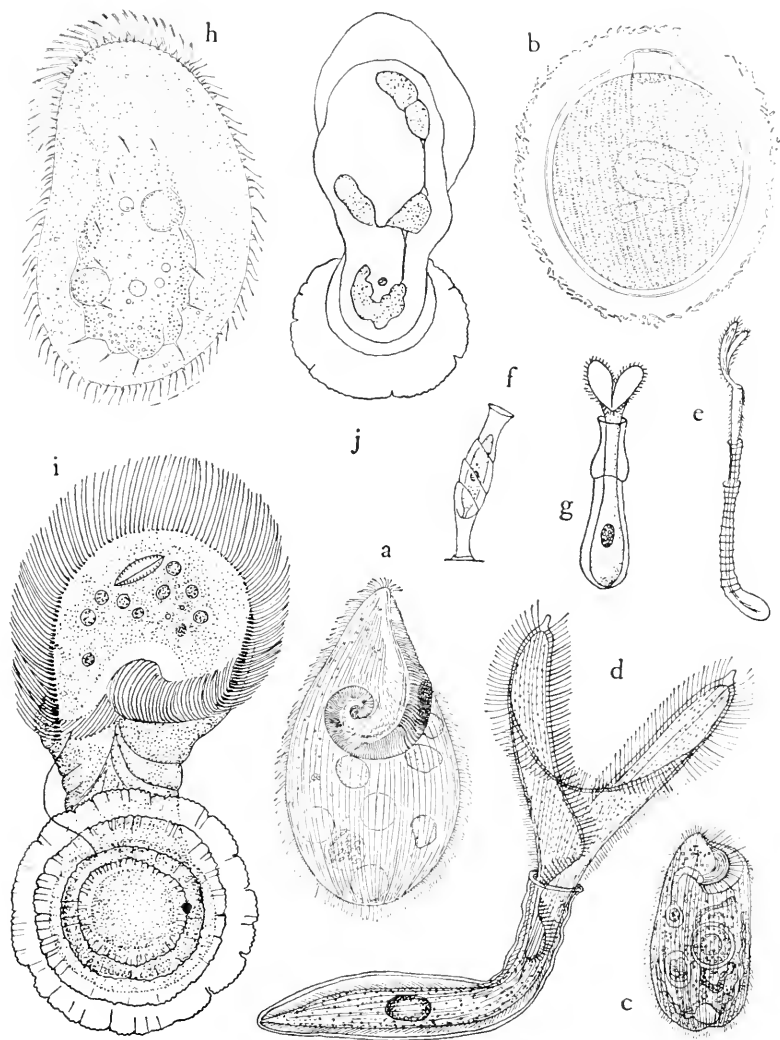


FIG. 265. a, b, *Fabrea salina* (a, $\times 170$; b, $\times 330$) (Kirby); c, *Climacostomum virens*, $\times 100$ (Stein); d, *Folliculina moebiusi*, $\times 170$ (Stein); e, *F. producta*, $\times 110$ (Wright); f, *Pseudofolliculina arctica*, $\times 50$ (Dons); g, *Parafolliculina violacea*, $\times 100$ (Dons); h, *Peritromus californicus*, $\times 360$ (Kirby); i, *Lichnophora macfarlandi*, $\times 420$ (Stevens); j, *L. conklini*, $\times 340$ (Stevens).

bearing spines (about 12μ long); 16–19 or more ventral ciliary rows; 2 spherical macronuclei, one anterior right and the other posterior left of hump; micronuclei 4 (2–5); $89\text{--}165\mu$ by $60\text{--}96\mu$; salt marsh pools with salinity 1.2–6 per cent in California.

P. emmae S. $90\text{--}100\mu$ long; creeping on bottom; Woods Hole.

Family 8 Licnophoridae Stevens

Genus **Licnophora** Claparède. Discoid; body roughly divisible into foot, neck and head; foot an attaching disc, with several concentric ciliary coronas; neck flattened, contractile narrowed part with or without a ventral furrow and fibril-bundles (both running from oral groove to foot); head highly flattened, round or ovoid; edge with membranellar zone which extends to pharyngeal funnel; macronucleus long chain-form; without contractile vacuole; free-swimming or commensal in fresh or salt water animals.

L. macfarlandi Stevens (Fig. 265, *i*). $140\text{--}180\mu$ long; attaching disc round; macronuclei in 25–35 parts in 4 groups; commensal in respiratory organs of *Holothuria californica*.

L. conklini S. (Fig. 265, *j*). $100\text{--}135\mu$ long; commensal in *Crepidula plana* of Atlantic coast.

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CHAPTER 38

Order 2 **Spirotricha** Bütschli (continued)

Suborder 2 **Oligotricha** Bütschli

THE cilia are greatly reduced in number in the Oligotricha and the adoral zone encloses a non-ciliated spiral peristomal field.

Free-living

Oral portion of peristome lies free on ventral surface.
 Family 1 Halteriidae

Adoral zone encloses frontal peristomal field in a closed spiral

Without lorica. Family 2 Strobilidiidae (p. 589)

With lorica or test. Family 3 Tintinnidiidae (p. 589)

Parasitic

Adoral and dorsal zones, both directed anteriorly and retractile; no other cilia. Family 4 Ophryoscolecidae (p. 590)

In addition to adoral and dorsal zones, groups of cirri in posterior half of body, directed posteriorly and nonretractile.
 Family 5 Cycloposthiidae (p. 596)

Family 1 **Halteriidae** Claparède et Lachmann

Genus **Halteria** Dujardin. Spherical or broadly fusiform; anterior border bears conspicuous adoral zone; oral part of peristome with a small membrane on right edge and cirri on left; with an equatorial zone of small oblique grooves, each bearing 3 long cirri or bristles; macronucleus oval; a micronucleus; contractile vacuole left of cytostome; fresh water. A few species.

H. grandinella (Müller) (Fig. 266, *a*). About 7 bristle-bearing grooves; 15 frontal and 7 adoral membranellae; 20–40 μ long. Kahl (1932) distinguishes 2 varieties: var. *cirrifera* (Fig. 266, *b*), 25–50 μ long, with huge cirri instead of fine body cirri; and var. *chlorelligera* (Fig. 266, *c*), 40–50 μ long, with bristles and large zoochlorellae; fresh water.

Genus **Strombidium** Claparède et Lachmann. Ovoid to spherical; adoral zone very conspicuous (2–4 conspicuous sickle-form frontal membranellae and adoral membranellae extend down cytopharynx, the first section surrounding an apical process); no body bristles or cirri; trichocysts; macronucleus oval or band-form; a micronucleus; a contractile vacuole; salt or fresh water. Numerous species.

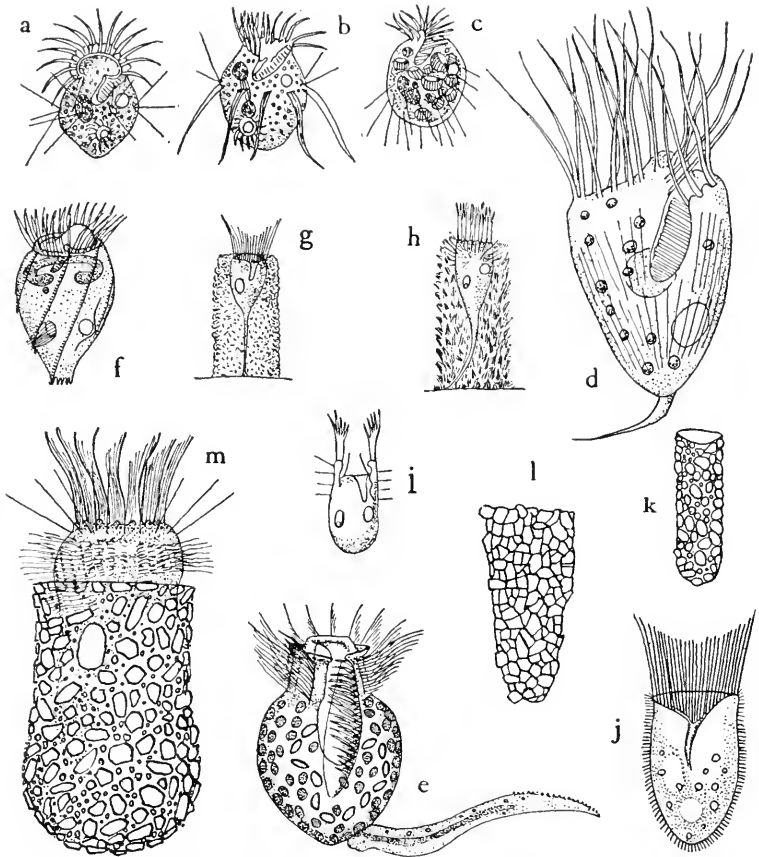


FIG. 266. a, *Halteria grandinella*, $\times 490$ (Kahl); b, *H. g.* var. *cirrifera*, $\times 370$ (Kahl); c, *H. g.* var. *chlorelligera*, $\times 260$ (Kahl); d, *Strombidium calkinsi*, $\times 900$ (Calkins); e, *Tontonia gracillima*, $\times 540$ (Fauré-Fremiet); f, *Strobilidium gyrans*, $\times 340$ (Kahl); g, *Tintinnidium fluviatile*, $\times 140$ (Kent); h, i, *T. semiciliatum*, $\times 140$ (Sterki); j, *Strombidinopsis gyrans*, $\times 270$ (Kent); k, *Tintinnopsis cylindrata*, $\times 440$ (Daday); l, *T. illinoisensis*, $\times 420$ (Hempel); m, *Codonella cratera*, $\times 540$ (Fauré-Fremiet).

S. calkinsi Fauré-Fremiet (Fig. 266, d). 35–60 μ long; brackish and salt water; Calkins (1902) first observed it at Woods Hole.

Genus **Tontonia** Fauré-Fremiet. With well-developed apical collar; a long cytoplasmic (contractile) caudal process; salt water.

T. gracillima F.-F. (Fig. 266, e). 48–52 μ long; caudal process 250–300 μ long; macronucleus moniliform; with zoochlorellae.

Family 2 **Strobilidiidae** Kahl

Genus **Strobilidium** Schewiakoff. Pyriform or turnip-shaped; cytostome at anterior end; without cytopharynx; horseshoe-shaped macronucleus anterior; a micronucleus; a contractile vacuole; fresh or salt water. Several species.

S. gyrans (Stokes) (Fig. 266, *f*). Lateral border with rounded elevation near anterior end, posterior end truncate; 40–70 μ long; in standing fresh water.

Family 3 **Tintinnidiidae** Claparède et Lachmann

Conical or trumpet-like, attached inside a lorica of various forms, composed of gelatinous or pseudochitinous substances; with longitudinal rows of cilia, and 2 (1–4) macro- and micro-nuclei; mostly pelagic, a few inhabiting fresh or brackish water. Kofoid and Campbell (1929) distinguished more than 300 species and placed them in 12 families and 51 genera, of which 23 genera were created by them. A few genera and species are mentioned here.

Genus **Tintinnidium** Kent. Elongated lorica, highly irregular in form; soft; aboral end closed or with a minute opening; wall viscous and freely agglomerates foreign bodies; salt or fresh water.

T. fluviatile (Stein) (Fig. 266, *g*). Lorica 100–200 μ by 45 μ ; on vegetation in fresh water.

T. semiciliatum (Sterki) (Fig. 266, *h, i*). 40–60 μ long; on plants in fresh water.

Genus **Strombidinopsis** Kent. Lorica often absent; ovate or pyriform; frontal border with numerous long cirrus-like cilia; body covered by fine cilia; contractile vacuole posterior; fresh water.

S. gyrans K. (Fig. 266, *j*). 30–80 μ long; fresh water pond.

Genus **Tintinnopsis** Stein. Lorica bowl-shaped; always with a broad aperture; aboral end closed; wall thin and covered with foreign bodies; salt or fresh water.

T. cylindrata Kofoid et Campbell (Fig. 266, *k*). Lorica 40–50 μ long; lake water.

T. illinoisensis Hempel (Fig. 266, *l*). Lorica 59 μ long; in river.

Genus **Codonella** Haeckel. Lorica urn- to pot-shaped; sharply divided externally and internally into a collar and bowl; collar without spiral structure; in fresh water.

C. cratera (Leidy) (Fig. 266, *m*). Lorica 60–70 μ by 40 μ ; a number of varieties are often mentioned.

Family 4 Ophryoscolecidae Stein

Elongate oval, asymmetrical; with 1 or 2 (adoral and dorsal) zones of membranellae; in digestive tract of mammals. Sharp (1914) instituted use of "forma" to distinguish forms in *Entodinium* with common characteristics differing in certain others, which scheme was extended to the whole family by Dogiel (1927). It is most probable that many species are varieties of a single species as judged by the work of Poljansky and Strelkow (1934); but since information is still incomplete, the present work ranks various formae with species, in agreement with Kofoed and MacLennan (1930).

Genus **Ophryoscolex** Stein. Ovoid; with adoral and dorsal zones of membranellae; dorsal zone some distance behind anterior end, encircling 3/4 the body circumference at middle, broken on right ventral side; 3 skeletal plates extend the body length on right-ventral side; 9–15 contractile vacuoles in 2 (anterior and posterior) circles; macronucleus simple, elongate; in stomach of cattle, sheep, goat and wild sheep (*Ovis orientalis cycloceros*). Several species. Dogiel (1927) designated the following species as 3 formae of *O. caudatus* Eberlein.

O. bicoronatus Dogiel (Fig. 267, *a*). 120–170 μ by 81–90 μ ; primary spine 38–58 μ long; in sheep.

O. caudatus Eberlein (Fig. 267, *b*). 137–162 μ by 80–98 μ ; preanal spines 47–60 μ long; in sheep, goat, and cattle.

O. quadricoronatus Dogiel (Fig. 267, *c*). 128–180 μ by 86–100 μ ; preanal spines 48–63 μ long; in sheep and *Ovis orientalis cycloceros*.

Genus **Caloscolex** Dogiel. Ovoid; anterior end truncate, posterior end rounded with or without processes; 2 zones of membranellae; dorsal zone encircles the body completely; 3 skeletal plates variously modified; 7 contractile vacuoles in a single circle; nucleus elongate; in stomach of *Camelus dromedarius*. Several species.

C. cuspidatus D. (Fig. 267, *d*). 130–160 μ by 73–90 μ .

Genus **Entodinium** Stein. Without dorsal zone; adoral zone at truncate anterior end; without skeleton; contractile vacuole anterior; macronucleus, cylindrical or sausage-form, dorsal; mi-

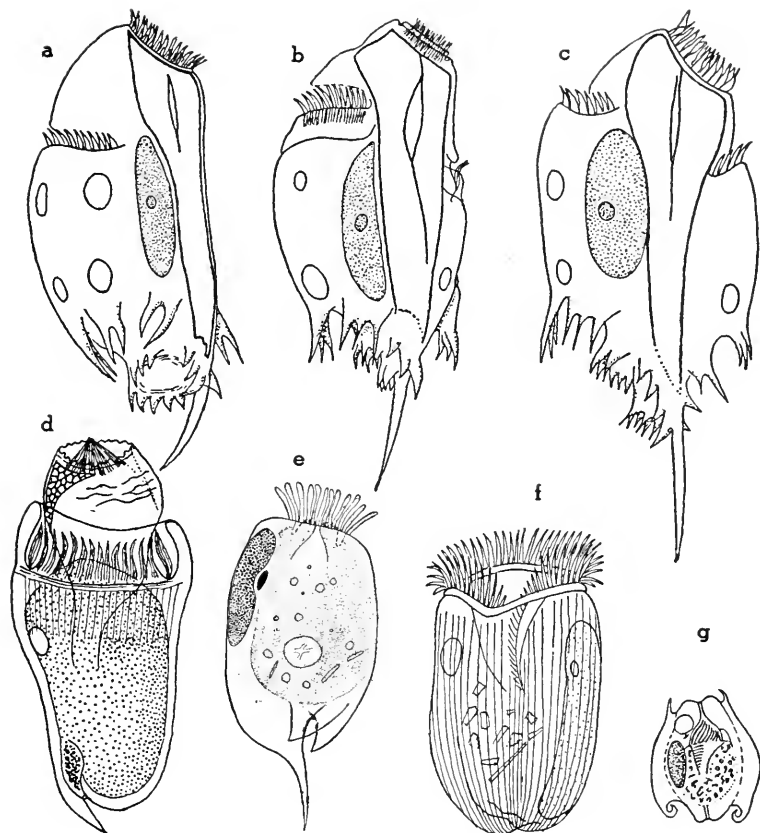


FIG. 267. a, *Ophryoscolex bicoronatus*, $\times 340$ (Dogiel); b, *O. caudatus*, $\times 310$ (Dogiel); c, *O. quadricoronatus*, $\times 340$ (Dogiel); d, *Caloscolex cuspidatus*, $\times 310$ (Dogiel); e, *Entodinium caudatum*, $\times 500$ (Becker and Talbott); f, *E. bursa*, $\times 390$ (Schuberg); g, *Amphacanthus ovum-rajae*, $\times 350$ (Dogiel).

cronucleus anterior to middle and on left-ventral side of macronucleus; in cattle and sheep. Numerous species.

E. caudatum S. (Fig. 267, e). $50\text{--}80\mu$ long; in cattle and sheep.

E. bursa S. (Fig. 267, f). $55\text{--}114\mu$ by $37\text{--}78\mu$ (Schuberg); 80μ by 60μ (Becker and Talbott); in stomach of cattle.

Genus **Amphacanthus** Dogiel. Similar to *Entodinium*; but spinous processes at both anterior and posterior ends; in stomach of *Camelus dromedarius*. One species.

A. ovum-rajae D. (Fig. 267, g). $46\text{--}55\mu$ by $32\text{--}48\mu$.

Genus **Eodinium** Kofoid et MacLennan. Dorsal zone on the same level as adoral zone; without skeleton; macronucleus a straight, rod-like body beneath dorsal surface; 2 contractile vacuoles; in cattle and sheep. Several species.

E. lobatum K. et M. (Fig. 268, *a*). $44\text{--}60\mu$ by $29\text{--}37\mu$; in *Bos indicus*.

Genus **Diplodinium** Schuberg. Adoral and dorsal zones on the same level; without skeletal plates; macronucleus beneath right side, its anterior third bent ventrally at an angle of $30^{\circ}\text{--}90^{\circ}$; 2 contractile vacuoles; in cattle, antelope, *Camelus dromedarius*, reindeer, goat, Numerous species.

D. dentatum (Stein) (Fig. 268, *b*). $65\text{--}82\mu$ by $40\text{--}50\mu$; in cattle (including *Bos indicus*).

Genus **Eremoplastron** Kofoid et MacLennan. Adoral and dorsal zones at anterior end; a single narrow skeletal plate beneath right surface; triangular or rod-like macronucleus, anterior end of which often bent ventrally; 2 contractile vacuoles; in cattle, antelope, sheep, reindeer. Numerous species.

E. bovis (Dogiel) (Fig. 268, *c*). $52\text{--}100\mu$ by $34\text{--}50\mu$; in cattle and sheep.

Genus **Eudiplodinium** Dogiel. Adoral and dorsal zones at anterior end; a single, narrow, skeletal plate beneath right surface; rod-like macronucleus with anterior end enlarged to form a hook opening dorsally; pellicle and ectoplasm thick; 2 contractile vacuoles with heavy membranes and prominent pores; in cattle.

E. maggii (Fiorentini) (Fig. 268, *d*). $104\text{--}255\mu$ by $63\text{--}170\mu$; in cattle, sheep and reindeer.

Genus **Diploplastron** Kofoid et MacLennan. Adoral and dorsal zones at anterior end; 2 skeletal plates beneath right surface; macronucleus narrow, rod-like; 2 contractile vacuoles below dorsal surface, separated from macronucleus. One species.

D. affine (Dogiel et Fedorowa) (Fig. 268, *e*). $88\text{--}120\mu$ by $47\text{--}65\mu$; in stomach of cattle, sheep, and goat.

Genus **Metadinium** Awerinzew et Mutafova. Adoral and dorsal zones at anterior end; 2 skeletal plates beneath right surface sometimes fused posteriorly; macronucleus with 2-3 dorsal lobes; 2 contractile vacuoles; pellicle and ectoplasm thick; conspicuous oesophageal fibrils beneath dorsal and right sides; in stomach of cattle, sheep, goat, and reindeer.

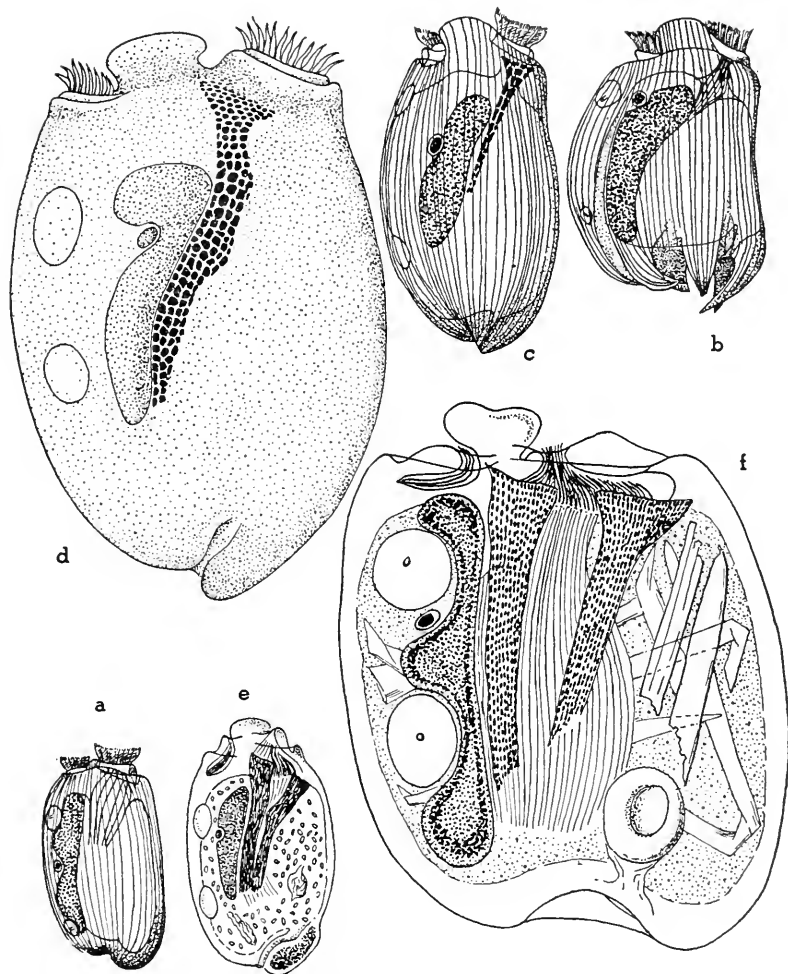


FIG. 268. a, *Eodinium lobatum*, $\times 540$ (Kofoid and MacLennan); b, *Diplodinium dentatum*, $\times 250$ (Kofoid and MacLennan); c, *Eremoplastron bovis*, $\times 550$ (Kofoid and MacLennan); d, *Eudiplodinium maggii*, $\times 500$ (Dogiel); e, *Diploplastron affine*, $\times 320$ (Dogiel); f, *Metadinium medium*, $\times 320$ (Dogiel).

M. medium A. et M. (Fig. 268, f). 180–272 μ by 111–175 μ ; in cattle.

Genus *Polyplastron* Dogiel. Adoral and dorsal zones at anterior end; 2 skeletal plates beneath right surface, separate or fused; 3

longitudinal plates beneath left surface, with anterior ends connected by cross bars; contractile vacuoles beneath dorsal surface in a longitudinal row, also with additional vacuoles; in stomach of cattle and sheep.

P. multivesiculatum (D. et Fedorowa) (Fig. 269, *a*). 120–190 μ by 78–140 μ ; in cattle and sheep. MacLennan (1934) found that the skeletal plates are made up of small, roughly prismatic blocks of glycogen, each with a central granule.

Genus **Elytroplastron** Kofoid et MacLennan. 2 zones at anterior end, 2 skeletal plates beneath right surface, a small plate beneath ventral surface, and a long plate below left side; pellicle and ectoplasm thick; conspicuous fibrils beneath dorsal and right sides. One species.

E. bubali (Dogiel) (Fig. 269, *b*). 110–160 μ by 67–97 μ ; in cattle, sheep, *Buffelus bubalus* and *Bos indicus*.

Genus **Ostracodinium** Dogiel. 2 zones at anterior end; broad skeletal plate beneath right side; 2–6 contractile vacuoles in a dorsal row; ecytopharyngeal fibrils thick, extend to posterior end; in cattle, sheep, antelope, steenbock, and reindeer, Numerous species.

O. dentatum (Fiorentini) (Fig. 269, *c*). 52–110 μ by 31–68 μ ; in stomach of cattle.

Genus **Enoploplastron** Kofoid et MacLennan. 2 zones near anterior end; 3 skeletal plates beneath right and ventral sides, either separate or partly fused; 2 contractile vacuoles; heavy pharyngeal fibrils; in cattle, reindeer and antelope.

E. triloricaum (Dogiel) (Fig. 269, *d*). Dogiel (1927) mentions size differences in those occurring in different host species, as follows: in cattle, 85–112 μ by 51–70 μ ; in reindeer, 75–103 μ by 40–58 μ ; in antelope (*Rhaphiceros* sp.), 60–110 μ by 37–56 μ .

Genus **Epidinium** Crawley. Elongate; twisted around the main axis; 2 zones; dorsal zone not at anterior end; 3 skeletal plates, with secondary plates; simple macronucleus club-shaped; 2 contractile vacuoles; in cattle, sheep, reindeer, camels, etc.

E. caudatum (Fiorentini) (Fig. 269, *e*). 113–151 μ by 45–61 μ ; in cattle, camels, *Cervus canadensis* and reindeer.

E. (Diplodinium) ecaudatum (F.) (Figs. 16; 269, *f*). 112–140 μ by 40–60 μ (Becker and Talbott); in cattle, sheep, and reindeer. The classical observation of Sharp (1914) on its neuromotor system has been described elsewhere (p. 55).

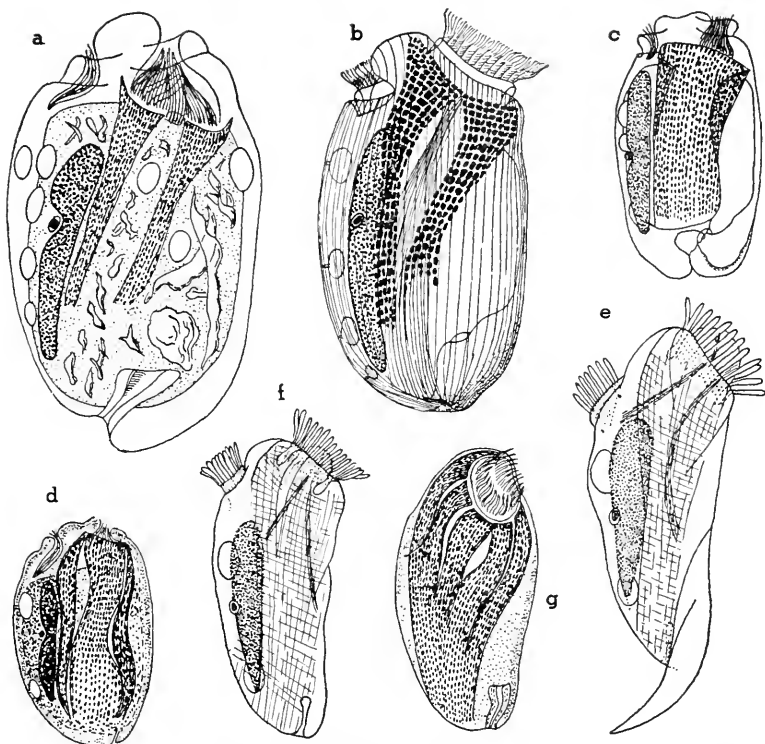


FIG. 269. a, *Polyplastron multivesiculatum*, $\times 360$ (Dogiel); b, *Elytroplastron bubali*, $\times 340$ (Dogiel); c, *Ostracodinium dentatum*, $\times 440$ (Dogiel); d, *Enoploplastron triloricaum*, $\times 370$ (Dogiel); e, *Epidinium caudatum*, $\times 340$ (Becker and Talbott); f, *E. ecaudatum*, $\times 340$ (Becker and Talbott); g, *Epiplastron africanum*, $\times 300$ (Dogiel).

Genus **Epiplastron** Kofoed et MacLennan. Elongate; 2 zones, dorsal zone behind anterior end; 5 skeletal plates, with secondary plates; macronucleus simple, elongate; 2 contractile vacuoles; in antelopes.

E. africanum (Dogiel) (Fig. 269, g). $90-140\mu$ by $30-55\mu$; in *Rhaphiceros* sp.

Genus **Ophisthotrichum** Buisson. 2 zones, dorsal zone at middle or near posterior end of body; one-piece skeletal plate well developed; 2 contractile vacuoles posterior; conjugation (Dogiel); in many African antelopes. One species.

O. janus (Dogiel) (*O. thomasi* B.) (Fig. 270, a). $90-150\mu$ by $42-60\mu$.

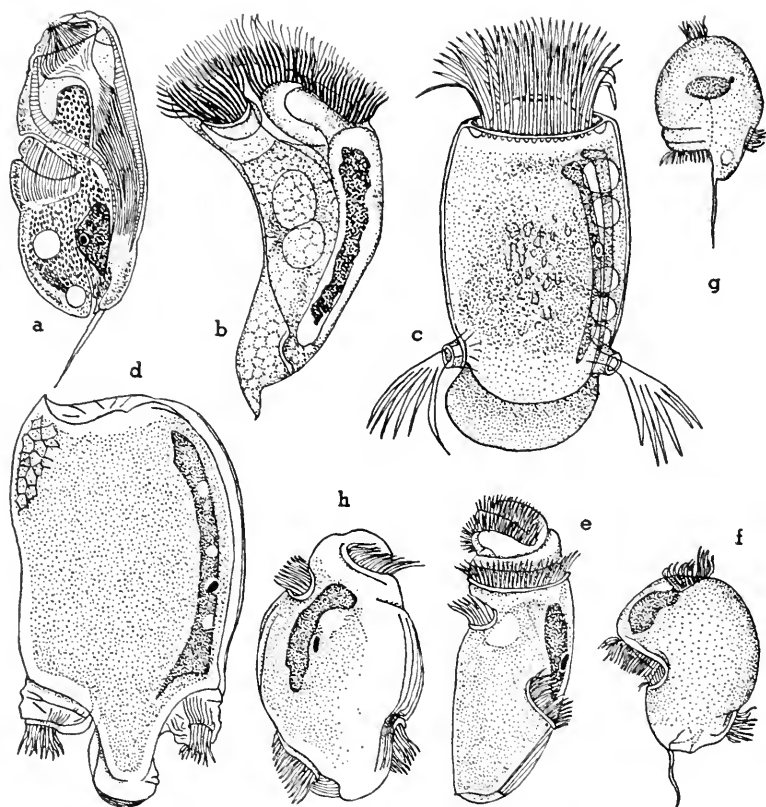


FIG. 270. a, *Ophisthotrichum janus*, $\times 370$ (Dogiel); b, *Cunhaia curvata*, $\times 670$ (Hasselmann); c, *Cycloposthium bipalmatum*, $\times 300$ (Bundle); d, *C. dentiferum*, $\times 270$ (Hsiung); e, *Spirodictinium equi*, $\times 270$ (Hsiung); f, *Triadinium caudatum*, $\times 300$ (Hsiung); g, *T. minimum*, $\times 440$ (Hsiung); h, *Tetratorum unifasciculatum*, $\times 280$ (Hsiung).

Genus **Cunhaia** Hasselmann. Cytostome near anterior end, with adoral zone; dorsal zone on 1/3 of anterior-dorsal surface; 2 contractile vacuoles; skeleton (?); in caecum of guinea pig, *Cavia aperea*. One species.

C. curvata H. (Fig. 270, b). 60–80 μ by 30–40 μ ; in Brazil.

Family 5 Cycloposthiidae Poche

Pellicle firm and body rigid; zones of membranellae at anterior and posterior ends; more or less compressed; cytopharynx short

and wide; macronucleus elongate; a single micronucleus; 2 or more contractile vacuoles; in horse and anthropoid apes.

Genus **Cycloposthium** Bundle. Large, elongate barrel-shaped; cytostome in center of a retractile conical elevation at anterior end; adoral zone conspicuous; an open ring-zone of membranellae near posterior end on both dorsal and ventral sides; pellicle ridged; skeleton club-shaped; several contractile vacuoles in a row along band-form macronucleus; in caecum and colon of horse. Many species.

C. bipalmatum (Fiorentini) (Fig. 270, c). $80\text{--}127\mu$ by $35\text{--}57\mu$.

C. dentiferum Gassovsky (Fig. 270, d). $140\text{--}222\mu$ by $80\text{--}110\mu$.

Genus **Spirodinium** Fiorentini. Elongate, more or less fusiform; adoral zone at anterior end; zone making at least one complete spiral near anterior end; posterior zone only half-spiral; in caecum and colon of horse. One species.

S. equi F. (Fig. 270, e). $77\text{--}180\mu$ by $30\text{--}74\mu$; widely distributed.

Genus **Triadinium** Fiorentini. More or less helmet-shaped; compressed; adoral zone at anterior end; 2 posterior (ventral and dorsal) zones; with or without a caudal projection; in caecum and colon of horse.

T. caudatum F. (Fig. 270, f). $59\text{--}86\mu$ by $50\text{--}68\mu$.

T. galea Gassovsky. $59\text{--}78\mu$ by $50\text{--}60\mu$.

T. minimum G. (Fig. 270, g). $35\text{--}58\mu$ by $30\text{--}40\mu$.

Genus **Tetratoxum** Gassovsky. Slightly compressed; 2 anterior and 2 posterior zones of membranellae; in colon of horse.

T. unifasciculatum (Fiorentini) (Fig. 270, h). $104\text{--}168\mu$ by $62\text{--}100\mu$; widely distributed.

T. escavatum Hsiung. $95\text{--}135\mu$ by $55\text{--}90\mu$.

T. parvum H. $67\text{--}98\mu$ by $39\text{--}52\mu$.

Genus **Tripalmaria** Gassovsky (*Tricaudalia* Buisson). Adoral zone at anterior end; 2 dorsal and 1 ventro-posterior zones in tuft-form; macronucleus inverted U-shape; in colon of horse.

T. dogieli G. (Fig. 271, a). $77\text{--}123\mu$ by $47\text{--}62\mu$.

Genus **Cochliatoxum** Gassovsky. Adoral zone near anterior end; 3 additional zones, 1 antero-dorsal, 1 postero-dorsal and 1 postero-ventral; macronucleus with curved anterior end; in colon of horse. One species.

C. periachtum G. (Fig. 271, b). $210\text{--}370\mu$ by $130\text{--}210\mu$.

Genus **Ditoxum** Gassovsky. Large adoral zone near anterior end; 2 dorsal (anterior and posterior) zones; macronucleus curved club-shaped; in colon of horse.

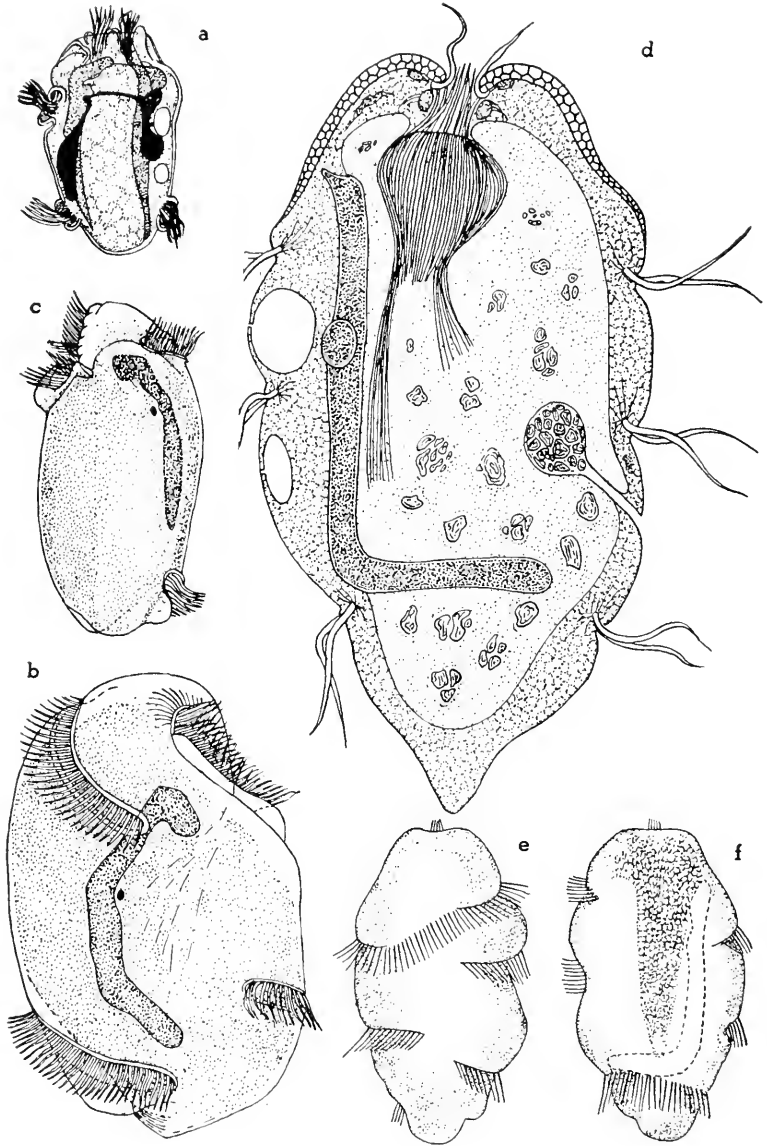


FIG. 271. a, *Tripalmaria dogieli*, $\times 180$ (Gassovsky); b, *Cochliatorum periachtum*, $\times 270$ (Hsiung); c, *Ditozum funinucleum*, $\times 270$ (Hsiung); d-f, *Troglodytella abrasarti* (d, $\times 670$ (Swezey); e, ventral and f, dorsal view, $\times 210$ (Brumpt and Joyeaux)).

D. funinucleum G. (Fig. 271, *c*). 135–203 μ by 70–101 μ .

Genus **Troglodytella** Brumpt et Joyeux. Ellipsoid; flattened; adoral zone; 3 additional zones (anterior zone continuous or not continuous on ventral surface; posterior zone continuous on dorsal surface; between them a small zone on each side); skeletal plates in anterior region; macronucleus L-form; contractile vacuoles in 2 circles; in colon of anthropoid apes.

T. abressarti B. et J. (Fig. 271, *d-f*). About 145–220 μ by 120–160 μ ; in colon of chimpanzees. Reichenow (1927) distinguished var. *acuminata* on the basis of drawn-out posterior end, which however was found by Swezey (1932) as simply a variant of *T. abressarti*.

T. gorillae Reichenow. 200–280 μ by 120–160 μ ; in colon of gorilla; with anterior zone not reaching the right side.

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CHAPTER 39

Order 2 **Spirotricha** Bütschli (continued)

Suborder 3 **Ctenostomata** Kahl

THE ciliates placed under this group are carapaced and compressed forms with a very sparse ciliation. The adoral zone is also reduced to about 8 membranellae. These organisms are exclusively free living and sapropelic in fresh, brackish, or salt water.

- Posterior half of carapace with 4 ciliated rows on left and at least 2 rows on right; with anterior row of cilia on left side near frontal edge.....Family 1 **Epalcidae**
- Posterior half of carapace with cirrus-like groups on left only, none on right; without frontal cilia
- Long ciliated band extends over both broad sides.....Family 2 **Discomorphidae** (p. 601)
- Short ciliated band ventral, extending equally on both broad sides.....Family 3 **Mylestomidae** (p. 602)

Family 1 **Epalcidae** Wetzel

Genus **Epalxis** Roux. Rounded triangular; anterior end pointed toward ventral surface, posterior end irregularly truncate; dorsal surface more convex; right carapace with 1 dorsal and 1 ventral ciliary row in posterior region; usually 4 (2-3) median teeth; all anal teeth without spine; with comb-like structures posterior to oral aperture; 1-2 oval macronuclei dorsal; contractile vacuole posterior-ventral; sapropelic in fresh or salt water. Many species.

E. mirabilis R. (Fig. 272, a). 38-45 μ by 27-30 μ ; fresh water.

Genus **Saprodinium** Lauterborn. Similar to *Epalxis*; but some of anal teeth (left and right) with spines; sapropelic in fresh or salt water. Several species.

S. dentatum L. (Fig. 272, b). 60-80 μ long; fresh water.

S. putrinum Lackey (Fig. 272, c). 50 μ long, 40 μ wide, about 15 μ thick; in Imhoff tanks.

Genus **Pelodinium** Lauterborn. Right carapace with 2 median rows of cilia, its median anal teeth fused into one so that there appear only three teeth. One species.

P. reniforme L. (Fig. 272, d). 40-50 μ long; sapropelic.

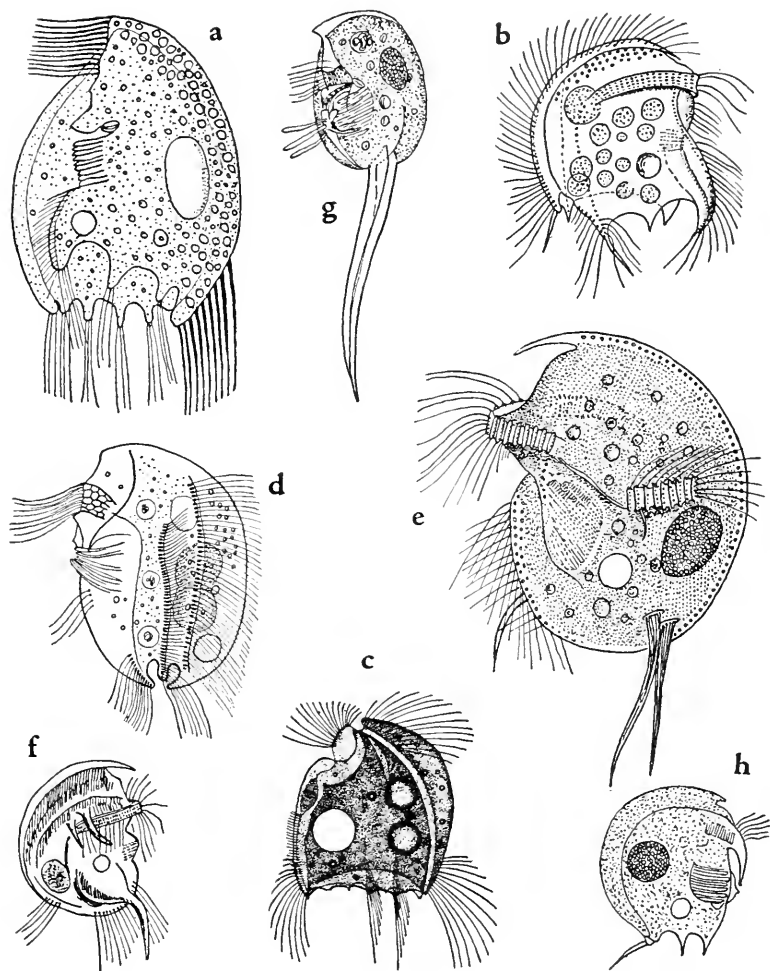


FIG. 272. a, *Epalxis mirabilis*, $\times 1200$ (Roux); b, *Saprodinium dentatum*, $\times 430$ (Kahl); c, *S. putrinum*, $\times 470$ (Lackey); d, *Pelodinium reniforme*, $\times 600$ (Lauterborn); e, f, *Discomorpha pectinata*, (e, $\times 500$; f, $\times 220$) (Kahl); g, *Mylestoma bipartitum*, $\times 470$ (Kahl); h, *Atopodinium fibulatum*, $\times 520$ (Kahl).

Family 2 Discomorphidae Poche

Genus **Discomorpha** Levander. Oval; ventrally directed anterior spine long; posterior end without teeth or ridges; ciliated

bands on both lateral surfaces; 2 spines on right side; 2 cirrus-like groups on posterior-left; sapropelic. A few species.

D. pectinata L. (Fig. 272, *e, f*). 70–90 μ long; sapropelic.

Family 3 Mylestomidae Kahl

Genus **Mylestoma** Kahl. Posterior margin without any indentation, though sometimes a small one on right side, but none on left; 3 often long ribbon-like cirri on peristome; fresh or salt water. Several species.

M. bipartitum (Gourret et Roesner) (Fig. 272, *g*). 35–50 μ long; salt water.

Genus **Atopodinium** Kahl. Posterior left side with one large, and right side with 2 indentations; macronucleus spherical; sapropelic.

A. fibulatum K. (Fig. 272, *h*). 40–50 μ long.

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CHAPTER 40

Order 2 **Spirotricha** Bütschli (continued)

Suborder 4 **Hypotricha** Stein

THE members of this suborder are, as a rule, flattened and strong cilia or cirri are restricted to the ventral surface. Except the family Aspidiscidae, the dorsal surface possesses rows of short slightly moveable tactile bristles. The peristome is very large with a well-developed adoral zone. The cirri on the ventral surface are called, according to their location, frontals, ventrals, marginals, anals (transversals), and caudals, as was mentioned before (Fig. 11, *b*). Asexual reproduction is by binary fission and sexual reproduction by conjugation (p. 148). Encystment is common. Mostly free-living in fresh, brackish or salt water; a few parasitic.

Adoral zone fully formed; dorsal surface with bristles

Ventrals in rows, though in some reduced; 2 rows of marginals. Family 1 Oxytrichidae

Ventrals and marginals not in longitudinal rows. Family 2 Euplotidae (p. 611)

Adoral zone reduced; without dorsal bristles. Family 3 Aspidiscidae (p. 613)

Family 1 **Oxytrichidae** Kent

Genus **Oxytricha** Ehrenberg (*Histrio* Sterki; *Opisthotricha* Kent; *Steinia* Diesing). Ellipsoid; flexible; ventral surface flattened, dorsal surface convex; 8 frontals; 5 ventrals; 5 anals; short caudals; marginals may or may not be continuous along posterior border; macronucleus in 2 parts, rarely single or in 4 parts; fresh or salt water. Numerous species.

O. fallax Stein (Fig. 273, *a*). Posterior region broadly rounded; about 150 μ long; fresh water.

O. bifaria Stokes (Fig. 273, *b*). Right side convex; left side flattened; posterior end pointed; about 250 μ long; fresh water infusion.

O. ludibunda S. (Fig. 273, *c*). Ellipsoid; flexible; 100 μ long; fresh water among sphagnum.

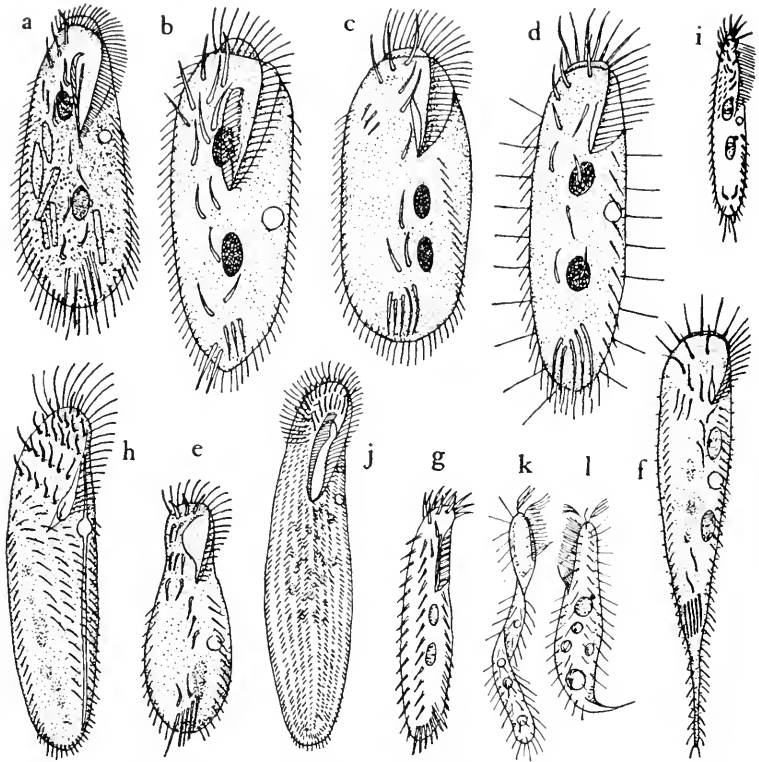


FIG. 273. a, *Oxytricha fallax*, $\times 230$ (Stein); b, *O. bifaria*, $\times 180$ (Stokes); c, *O. ludibunda*, $\times 400$ (Stokes); d, *O. setigera*, $\times 870$ (Stokes) e, *Tachysoma parvistyla*, $\times 490$ (Stokes); f, *Urosoma caudata*, $\times 250$ (Stokes); g, *Amphisiella thiophaga*, $\times 380$ (Kahl); h, *Eschaneustyla brachytoma*, $\times 240$ (Stokes); i, *Gonostomum strenuum*, $\times 160$ (Engelmann); j, *Hemicyclostyla sphagni*, $\times 100$ (Stokes); k, l, *Cladotricha koltzowii* (k, $\times 170$; l, $\times 300$) (Kahl).

O. setigera S. (Fig. 273, d). Elongate ellipsoid; 5 frontals; ventrals shifted anteriorly; 50μ long; fresh water.

Genus **Tachysoma** Stokes (*Actinotricha* Cohn). Flexible; frontals 8–10, of which anterior three are usually the largest; 5 ventrals scattered; 5 anals; marginals at some distance from lateral borders, interrupted posteriorly; fresh or salt water.

T. parvistyla S. (Fig. 273, e). 10 frontals scattered; about 63μ long; in shallow freshwater pools.

Genus **Urosoma** Kowalewski. Similar to *Oxytricha*; but posterior portion drawn out and much narrowed; fresh water.

U. caudata (Stokes) (Fig. 273, f). 200–250 μ long; pond water.

Genus **Amphisiella** Gourret et Roeser. With a single row of ventrals and 2 marginal rows; salt or fresh water. Several species.

A. thiophaga (Kahl) (Fig. 273, g). 70–100 μ long; salt water.

Genus **Eschaneustyla** Stokes. Elliptical or ovate; narrow peristome 1/3 the body length; frontals numerous, about 22 in addition to 2 at anterior margin; ventrals small and numerous in 3 oblique rows; no anals; marginals uninterrupted; contractile vacuole a long canal near left border; fresh water. One species.

E. brachytona S. (Fig. 273, h). 170–220 μ long.

Genus **Gonostomum** Sterki (*Plagiotricha* Kent). Flexible; 8 or more frontals; 1–2 oblique ventral rows of short cirri; 4 or 5 caudals; 2 marginal rows; fresh water.

G. strenuum (Engelmann) (Fig. 273, i). Elongate; with caudal bristles; about 150 μ long; fresh water.

Genus **Hemicyclostyla** Stokes. Elongate oval; flexible; ends rounded; 20 or more frontals, arranged in 2 semicircular rows; adoral row begins near center of right side of peristomal field; ventral surface entirely covered with fine cilia; no anals; one or more contractile vacuoles; nucleus distributed; fresh water.

H. sphagni S. (Fig. 273, j). About 400–500 μ long; marsh water with sphagnum.

Genus **Hypotrichidium** Ilowaisky. 2 ventral rows of cirri and marginals spirally arranged; peristome large, extends 1/2 the body length, with a large undulating membrane; 2 macro- and micro-nuclei; contractile vacuole anterior-left; fresh water.

H. conicum I. (Fig. 274, a). 90–150 μ long.

Genus **Cladotricha** Gajevskaja. Elongate band-form; anterior end rounded, posterior end rounded or attenuated; frontals only 2 feathery cirri; macronucleus spheroidal; micronucleus; without contractile vacuole; salt water, with 5–20 per cent salt content. One species.

C. koltzowii G. (Fig. 273, k, l). Band-form up to about 200 μ long; posteriorly attenuated forms up to about 100 μ long.

Genus **Psilotricha** Stein. Oval to ellipsoid; frontals and anals undifferentiated; ventrals and marginals long bristles, few; ventrals in 2 rows and a rudimentary row toward left; with or without zoochlorellae; fresh water. A few species.

P. acuminata S. (Fig. 274, b). 80–100 μ long.

Genus **Kahlia** Horvath. Frontal margin with 3–4 strong cirri; 5–8 ventral longitudinal rows; marginals; sapropelic in fresh water.

K. acrobates H. (Fig. 274, c). 100–200 μ long; soil infusion.

Genus **Uroleptus** Ehrenberg. Elongate body drawn out into a tail-like portion, 3 frontals; 2–4 rows of ventral cirri; marginals; no anals; sometimes rose- or violet-colored; fresh or salt water. Many species.

U. limnetis Stokes (Fig. 274, d). About 200 μ long; fresh water among vegetation.

U. longicaudatus S. (Fig. 274, e). About 200 μ long; marsh water with sphagnum.

U. dispar S. (Fig. 274, f). 150–170 μ long; fresh water.

U. halseyi Calkins (Fig. 276, a). About 160 μ by 20 μ ; peristome 1/6–1/7 the body length; 3 ventrals; macronucleus divided into many (up to 26) parts; 2 (1–3) large macronuclei; fresh water.

Genus **Uroleptopsis** Kahl. Ventrals in 2 uninterrupted rows; salt water. A few species.

U. citrina K. (Fig. 274, g). Elongate; flexible; ectoplasm with pale-yellow ringed bodies which give the organism yellowish color; marginals discontinuous posteriorly; 2 contractile vacuoles near left border; nucleus distributed (?); 150–250 μ long; salt water.

Genus **Strongylidium** Sterki. 2–5 ventral rows of cirri, marginals spirally arranged; 3–6 frontals; 2–many macronuclei; fresh or salt water. Many species.

S. californicum Kahl (Fig. 274, h). 4–5 frontals; macronuclei about 30 in number; 4 micronuclei; contractile vacuole with short canals; about 250 μ long; fresh water among vegetation.

Genus **Stichotricha** Perty. Slender ovoid or fusiform; peristome-bearing part narrowed; not flexible; usually 4 spiral rows of cirri; sometimes tube-dwelling, and then in groups; fresh or salt water. Many species.

S. secunda P. (Fig. 274, i). 130–200 μ long; in fresh water.

Genus **Chaetospira** Lachmann. Similar to *Stichotricha*; but peristome-bearing part flexible; fresh or salt water.

C. mulleri L. 150–250 μ long; in lorica; fresh water.

Genus **Urostyle** Ehrenberg. Ellipsoid; flexible; ends rounded; flattened ventral surface with 4–10 rows of small cirri and 2 marginal rows; 3 or more frontals; 5–12 anals; macronucleus a single body or in many parts; fresh or salt water. Numerous species.

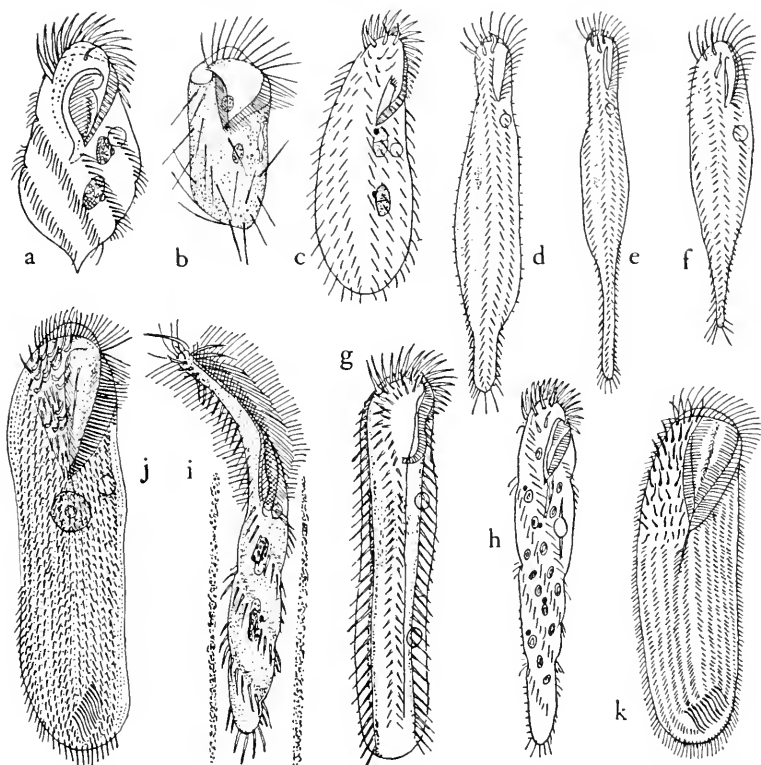


FIG. 274. a, *Hypotrichidium conicum*, $\times 200$ (Kahl); b, *Psilotricha acuminata*, $\times 230$ (Stein); c, *Kahlia acrobates*, $\times 240$ (Kahl); d, *Uroleptus limnetis*, $\times 240$ (Stokes); e, *U. longicaudatus*, $\times 240$ (Stokes); f, *U. dispar*, $\times 240$ (Stokes); g, *Uroleptopsis citrina*, $\times 260$ (Kahl); h, *Strongylidium californicum*, $\times 200$ (Kahl); i, *Stichotricha secunda*, $\times 340$ (Kahl); j, *Urostyla grandis*, $\times 140$ (Stein); k, *U. trichogaster*, $\times 150$ (Kahl).

U. grandis E. (Figs. 45; 274, j). 300–400 μ long; macronucleus in 100 or more parts; 6–8 micronuclei; fresh water.

U. trichogaster Stokes (Fig. 274, k). 250–330 μ long; fresh water.

U. caudata S. (Fig. 275, a). Elongate ellipsoid; flexible; narrowed anterior part bent to left; peristome $1/3$ the body length; macronucleus in many parts; contractile vacuoles on left margin; about 600 μ long; fresh water with sphagnum.

Genus **Kerona** Ehrenberg. Reniform; no caudals; 6 oblique rows of ventral cirri; commensal. One species.

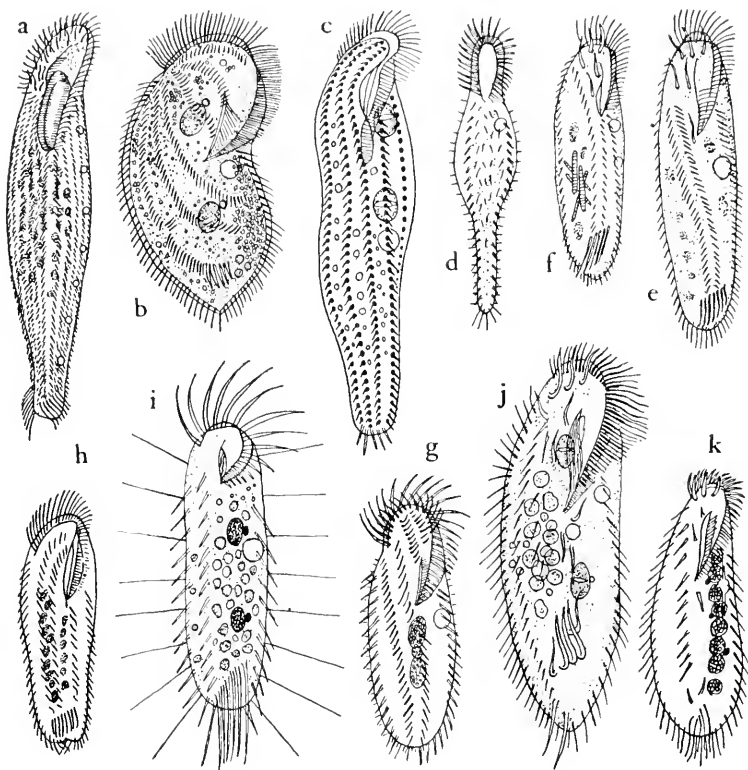


FIG. 275. a, *Urostyla caudata*, $\times 90$ (Stokes); b, *Kerona polyporum*, $\times 200$ (Stein); c, *Keronopsis rubra*, $\times 270$ (Entz); d, *Epiclintes pluviialis*, $\times 100$ (Smith); e, *Holosticha vernalis*, $\times 220$ (Stokes); f, *H. hymenophora*, $\times 180$ (Stokes); g, *Paraholosticha herbicola*, $\times 200$ (Kahl); h, *Trichotaxis stagnatilis*, $\times 190$ (Stokes); i, *Balladyna elongata*, $\times 800$ (Roux); j, *Pleurotricha lanceolata*, $\times 250$ (Stein); k, *Gastrostyla muscorum*, $\times 200$ (Kahl).

K. polyporum E. (Fig. 275, b). 120–200 μ long; commensal on *Hydra*.

Genus **Keronopsis** Penard. 2 ventral rows of cirri reaching frontal field; caudals variable; macronucleus usually in several (rarely 2) parts; fresh or salt water. Numerous species.

K. rubra (Ehrenberg) (Fig. 275, c). Reddish; 200–300 μ long; salt water.

Genus **Epiclintes** Stein. Elongate; spoon-shaped; flattened ven-

tral surface with more than 2 rows of cirri; 2 marginal rows; frontals undifferentiated; anals; no caudals; salt or fresh water. A few species.

E. pluvialis Smith (Fig. 275, *d*). About 375μ long; fresh water.

Genus **Holosticha** Wrzesniowski. 3 of frontals along anterior margin; 2 ventral and 2 marginal rows of cirri; anals; fresh or salt water. Numerous species.

H. vernalis Stokes (Fig. 275, *e*). 7 anals; about 180μ long; shallow pools with algae.

H. hymenophora S. (Fig. 275, *f*). 5 anals; 2 contractile vacuoles; $160\text{--}200\mu$ long; shallow pools.

Genus **Paraholosticha** Kahl. Elongate-oval; flexible; ventral cirri in 2 parallel oblique rows; with a row of stiff cirri along frontal margin, posterior to it 2 short rows of cirri; marginals continuous or interrupted at posterior border; fresh water.

P. herbicola K. (Fig. 275, *g*). $150\text{--}190\mu$ long; fresh water among algae.

Genus **Trichotaxis** Stokes. Similar to *Holosticha*; but with 3 rows of ventral cirri; fresh or salt water.

T. stagnatilis S. (Fig. 275, *h*). About 160μ long; ellipsoid; in fresh water among decaying vegetation.

Genus **Balladyna** Kowalewski. Ellipsoid; frontals not well developed or lacking; 1 ventral and 2 marginal rows of cirri; long dorsal and lateral bristles; fresh water.

B. elongata Roux (Fig. 275, *i*). $32\text{--}35\mu$ by $11\text{--}12\mu$; fresh water among plants and detritus.

Genus **Pleurotricha** Stein. Oblong to ellipsoid; marginals continuous; 8 frontals; 3–4 ventrals; 7 anals of which 2 are more posterior; 2 rows of ventral cirri; between ventrals and marginals 1–3 rows of few coarse cilia; fresh water.

P. lanceolata (Ehrenberg) (Fig. 275, *j*). $100\text{--}165\mu$ long; 2 macro- and 2 micro-nuclei; Manwell (1928) studied its conjugation, division, encystment and nuclear variation.

Genus **Gastrostyla** Engelmann. Frontals distributed except 3 along the frontal margin; ventrals irregular; 5 anals; macronucleus divided into 2–8 parts; fresh or salt water.

G. muscorum Kahl (Fig. 275, *k*). $130\text{--}200\mu$ long; macronucleus in 8 parts; fresh water in vegetation.

Genus **Stylonychia** Ehrenberg. Ovoid to reniform; not flexible; ventral surface flat, dorsal surface convex; 8 frontals; 5 ventrals;

5 anals; marginals; 3 caudals; with short dorsal bristles; fresh or salt water. Many species.

S. mytilus (Müller) (Fig. 276, b). 100–300 μ long; fresh, brackish and salt water.

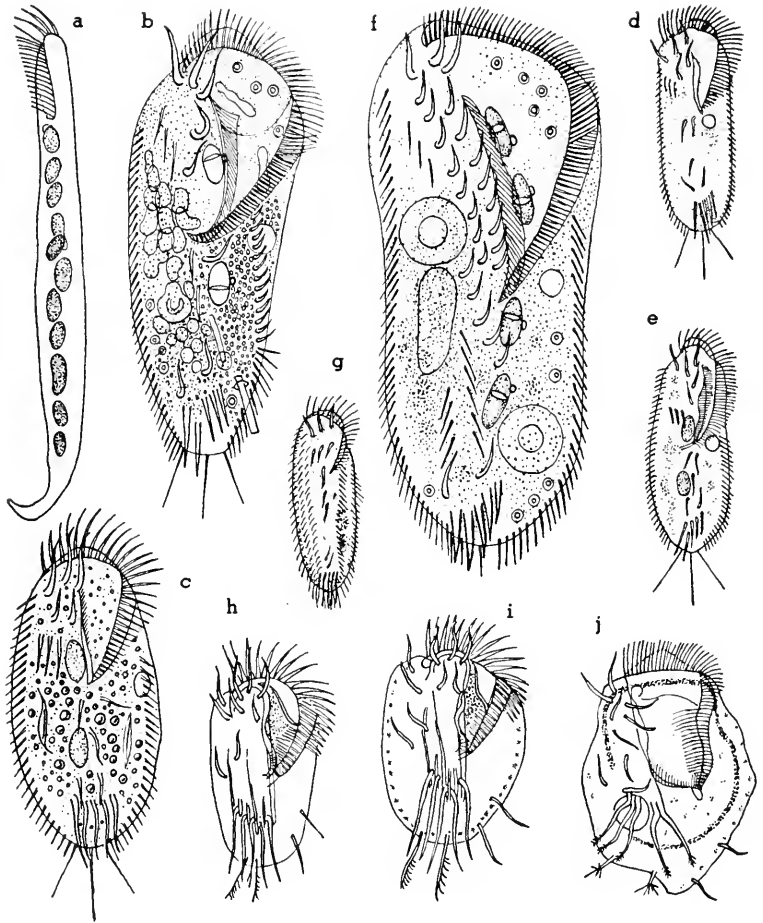


FIG. 276. a, *Uroleptus halseyi*, $\times 470$ (Calkins); b, *Stylonychia mytilus*, $\times 200$ (Stein); c, *S. pustulata*, $\times 400$ (Roux); d, *S. putrina*, $\times 200$ (Stokes); e, *S. notophora*, $\times 200$ (Stokes); f, *Onychodromus grandis*, $\times 230$ (Stein); g, *Onychodromopsis flexilis*, $\times 240$ (Stokes); h, i, *Euplotes patella*, $\times 290$ (Kahl); j, *E. plumipes*, $\times 270$ (Stokes).

S. pustulata E. (Fig. 276, c). About 150 μ long; fresh water; nuclear changes studied by Summers (1935).

S. putrina Stokes (Fig. 276, *d*). 125–150 μ long; fresh water.

S. notophora S. (Fig. 276, *c*). About 125 μ long; standing water.

Genus **Onychodromus** Stein. Not flexible; somewhat rectangular; anterior end truncate, posterior end rounded; ventral surface flat, dorsal surface convex; peristome broadly triangular in ventral view; 3 frontals; 3 rows of cirri parallel to right edge of peristome; 5–6 anals; marginals uninterrupted; 4–8 macronuclei; contractile vacuole; fresh water. One species.

O. grandis S. (Fig. 276, *f*). 100–300 μ long.

Genus **Onychodromopsis** Stokes. Similar to *Onychodromus*; but flexible; 6 frontals of which the anterior three are the largest; fresh water. One species.

O. flexilis S. (Fig. 276, *g*). 90–125 μ long; standing pond water.

Family 2 Euplotidae Claus

Genus **Euplotes** Ehrenberg. Inflexible body ovoid; ventral surface flattened, dorsal surface convex; longitudinally ridged; peristome broadly triangular; frontal part of adoral zone lies in flat furrow; 9 or more frontal-ventrals; 5 anals; 4 scattered caudals; macronucleus band-like; a micronucleus; contractile vacuole posterior; fresh or salt water. Numerous species.

E. patella (Müller) (Figs. 11, *a*; 12; 17; 51; 276, *h, i*). 9 frontal-ventrals; polymorphic; about 80–150 μ long; fresh and salt water (experimentally by Bullington). Its neuromotor system studied by Yocom (1918), Taylor (1920) and Turner (1933) (p. 55–56); macronuclear division, by Turner (1930) (p. 120).

E. plumipes Stokes (Fig. 276, *j*). About 125 μ long; fresh water.

E. carinatus S. (Fig. 277, *a*). About 70 μ by 50 μ ; fresh water.

E. charon (Müller) (Fig. 277, *b*). 70–90 μ long; salt water.

Genus **Euplotidium** Noland. Cylindrical; 9 frontal-ventrals in 2 rows toward right; 5 anals; a groove extends backward from oral region to ventral side, in which the left-most anal cirrus lies; peristome opened widely at anterior end, but covered posteriorly by a transparent, curved, flap-like membrane; adoral zone made up of about 80 membranellae; longitudinal ridges (carinae) 3 dorsal and 2 lateral; a row of protrichocysts under each carina; a broad zone of protrichocysts in antero-dorsal region; cytoplasm densely granulated; salt water. One species.

E. agitatum N. (Fig. 277, *c, d*). 65–95 μ long; erratic movement rapid; observed in half-dead sponges in Florida.

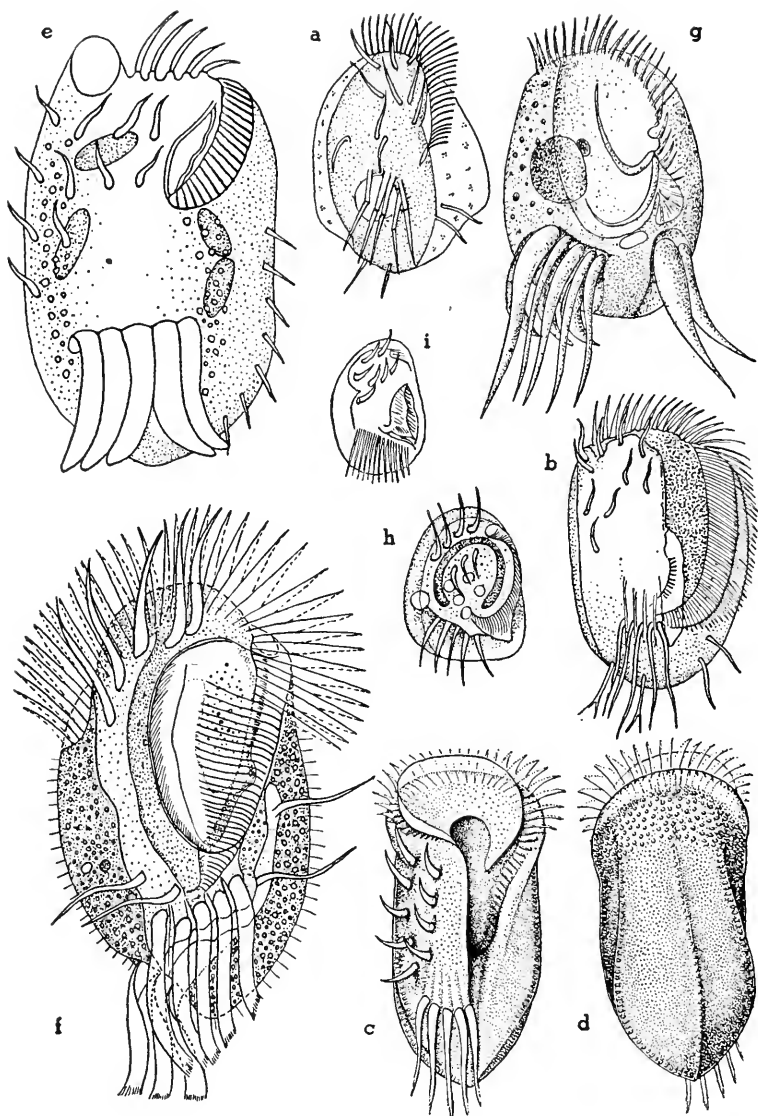


FIG. 277. a, *Euplotes carinatus*, $\times 430$ (Stokes); b, *E. charon*, $\times 440$ (Kahl); c, d, *Euplotidium agitatum*, $\times 540$ (Noland); e, *Certesiea quadrinucleata*, $\times 670$ (Sauerbrey); f, *Diophrys appendiculatus*, $\times 570$ (Wallengren); g, *Uronychia setigera*, $\times 870$ (Calkins); h, *Aspidisca lynceus*, $\times 300$ (Stein); i, *A. polystyla*, $\times 290$ (Kahl).

Genus **Certesia** Fabre-Domergue. Ellipsoid; flattened; dorsal surface slightly convex, ventral surface flat or concave; 5 frontals at anterior border; 7 ventrals; 5 anals; no caudals; marginals small in number; 4 macronuclei; salt water. One species.

C. quadrinucleata F.-D. (Fig. 277, *e*). 70–100 μ by about 45 μ .

Genus **Diophrys** Dujardin. Peristome relatively large, often reaching anals; 7–8 frontal-ventrals; 5 anals; 3 strong cirri right-dorsal near posterior margin; salt water.

D. appendiculatus (Ehrenberg) (Fig. 277, *f*). 60–100 μ long; salt water; Woods Hole (Calkins).

Genus **Uronychia** Stein. Without frontals and ventrals; 5 anals; 3 right-dorsal cirri (as in *Diophrys*); 2 left-ventral cirri near posterior margin; peristome, oval with a large undulating membrane on right edge; salt water. Several species.

U. setigera Calkins (Fig. 277, *g*). 40 μ by 25 μ ; salt water; Woods Hole.

Family 3 Aspidiscidae Claus

Genus **Aspidisca** Ehrenberg. Small; ovoid; inflexible; right and dorsal side convex, ventral side flattened; adoral zone reduced or rudimentary; 7 frontal-ventrals; 5–12 anals; macronucleus horse-shoe-shaped or occasionally in 2 rounded parts; contractile vacuole posterior; fresh or salt water. Numerous species.

A. lynceus E. (Figs. 52; 277, *h*). 30–50 μ long; fresh water. Division studied by Summers (1935).

A. polystyla Stein (Fig. 277, *i*). About 50 μ long; salt water; Woods Hole (Calkins).

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Order 3 **Chonotricha** Wallengren

THESE ciliates live attached to aquatic animals, especially crustaceans and have developed a peculiar organization. The body is, as a rule, vase-form with an apical peristome, around which extends a more or less complicated ectoplasmic collar or funnel and along which are found ciliary rows that lead to the deeply located cytostome and cytopharynx. The macronucleus is oval and situated centrally; there is a contractile vacuole usually near the cytopharynx. Asexual reproduction is by lateral budding, and conjugation has been observed in a few species.

Family **Spirochonidae** Stein

Genus **Spirochona** Stein. Peristome funnel spirally wound; ciliary zone on floor of spiral furrow; attached to *Gammarus* in fresh water. Several species. Szwarczewsky (1928) described several species from Lake Baikal in Siberia.

S. gemmipara S. (Fig. 278, a). 80–120 μ long; attached to gill-plates of *Gammarus pulex* and other species.

Genus **Stylochona** Kent. Peristomal funnel with an inner funnel. One species.

S. coronata K. (Fig. 278, b). About 60 μ long on marine *Gammarus*.

Genus **Kentrochona** Rompel (*Kentrochonopsis* Doflein). Peristomal funnel wide, simple, membranous; with or without a few (2) spines.

K. nebaliae R. (Fig. 278, c). About 40 μ long; much flattened, with its broad side attached by means of gelatinous substance to epi- and exo-podite of *Nebalia geoffroyi*; salt water.

Genus **Heliochona** Plate. Peristomal funnel with numerous needle-like spines.

H. scheuteni (Stein) (Fig. 278, d). About 80–90 μ long; on appendages of *Gammarus locusta*; salt water.

H. sessilis P. (Fig. 278, e). About 60 μ long; on *Gammarus locusta*; salt water.

Genus **Chilodochona** Wallengren. Peristome drawn out into 2 lips; with a long stalk.

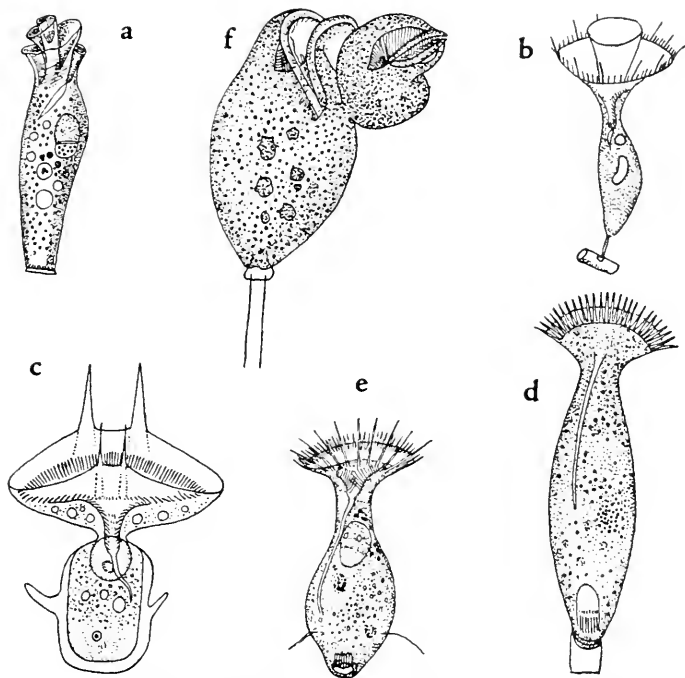


FIG. 278. a, *Spirochona gemmipara*, $\times 300$ (Hertwig); b, *Stylochona coronata*, $\times 400$ (Kent); c, *Kentrochona nebaliae*, $\times 970$ (Rompel); d, *Heliochona scheuteni*, $\times 550$ (Wallengren); e, *H. sessilis*, $\times 510$ (Wallengren); f, *Chilodochona quennerstedti*, $\times 400$ (Wallengren).

C. quennerstedti W. (Fig. 278, f). 60–115 μ long; stalk, 40–160 μ ; on *Ebalia turnefacta* and *Portunus depurator*; salt water.

Reference

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CHAPTER 42

Order 4 **Peritricha** Stein

THE peritrichous ciliates possess a much enlarged disk-like anterior region which is conspicuously ciliated. The adoral zone is counter-clockwise to the eytostome viewed from the anterior end. The body ciliation is more or less limited. The stalked forms produce free-swimming individuals, **telotrochs**. Asexual reproduction is by binary fission; and conjugation occurs commonly. The majority are free-living, often attached to various aquatic animals and plants, although a few are parasitic.

Attached to submerged objects; usually no body cilia, though telotroch possesses a posterior ring of cilia. Suborder 1 Sessilia
Free-swimming; but with highly developed attaching organellae on aboral end which are ciliated permanently.
. Suborder 2 Mobilia (p. 625)

Suborder 1 **Sessilia** Kahl

Without lorica, although some with a gelatinous or mucilaginous envelope. Tribe 1 Aloricata
With definite pseudochitinous lorica. Tribe 2 Loricata (p. 623)

Tribe 1 **Aloricata** Kahl

Posterior end with 1–2 short spines; swimming with peristome-bearing end forward. Family 1 Astylozoonidae
Posterior end, directly or indirectly through stalk, attached to submerged objects
Anterior region a long cylindrical, highly contractile neck; contractile vacuole posterior, connected with vestibule by a long canal; reservoir of contractile vacuole distinct; with or without a thin stalk. Family 2 Ophryidiidae (p. 618)
Anterior portion not drawn out into a neck
Without stalk. Family 3 Scyphidiidae (p. 618)
With stalk
Stalk non-contractile. Family 4 Epistylidae (p. 619)
Stalk contractile. Family 5 Vorticellidae (p. 621)

Family 1 **Astylozoonidae** Kahl

Genus **Astylozoon** Engelmann (*Geleicella* Stiller). Free-swimming; pyriform or conical; aboral end attenuated, with 1–2

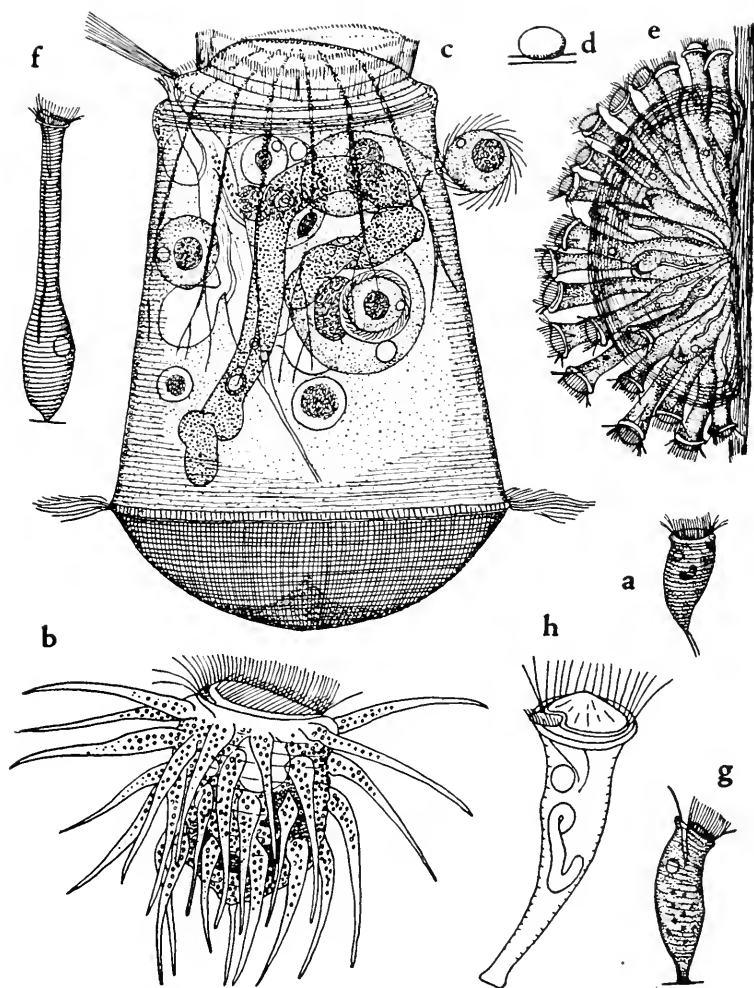


FIG. 279. a, *Astylozoon fallax*, $\times 170$ (Engelmann); b, *Hastatella aesculacantha*, $\times 580$ (Jarocki); c, *Opisthonecta henneguyi*, $\times 500$ (Lynch and Noble); d, e, *Ophridium sessile* (d, $\times 1.5$; e, $\times 65$) (Kent); f, *O. vernalis*, $\times 160$ (Stokes); g, *Scyphidia constricta*, $\times 360$ (Stokes); h, *Paravorticella clymenellae*, $\times 65$ (Shumway).

thigmotactic bristles; pellicle smooth or furrowed; with or without gelatinous envelope; in fresh water. A few species.

A. fallax E. (Fig. 279, a). 70–100 μ ; fresh water.

Genus **Hastatella** Erlanger. Free-swimming; body surface with 2–4 rings of long conical ectoplasmic processes; fresh water.

H. aesculacantha Jarocki et Jacobowska (Fig. 279, b). 30–52 μ by 24–40 μ ; in stagnant water.

Genus **Opisthonecta** Faurè-Fremiet. Conical; ends broadly rounded; a ring of long cilia close to aboral end; adoral zone about 1.1 turns, composed of 2 parallel rows; a papilla with about 12 long cilia, just above the opening into vestibule; macronucleus sausage-form; micronucleus; 3 contractile vacuoles connected with cytopharynx; fresh water. One species.

O. henneguyi F.-F. (Fig. 279, c). 148–170 μ long. The organisms studied by Lynch and Noble (1931) were infected by endoparasitic suctorian, *Endosphaera engelmanni* (p. 638).

Family 2 Ophryidiidae Kent

Genus **Ophrydium** Ehrenberg (*Gerda* Claparède et Lachmann). Cylindrical with a contractile neck; posterior end pointed or rounded; variable number of individuals in a common mucilaginous mass; pellicle usually cross-striated; fresh water.

O. sessile Kent (Fig. 279, d, e). Fully extended body up to 300 μ long; colorless or slightly brownish; ovoid colony up to 5 mm. by 3 mm.; attached to freshwater plants.

O. vernalis (Stokes) (Fig. 279, f). About 250 μ long; highly contractile; in shallow freshwater ponds in early spring (Stokes).

Family 3 Scyphidiidae Kahl

Genus **Scyphidia** Dujardin. Cylindrical; posterior end attached to submerged object by an attaching disk; cross-striated; fresh or salt water.

S. constricta Stokes (Fig. 279, g). About 55–60 μ long; pond water.

Genus **Paravorticella** Kahl. Similar to *Scyphidia*; but posterior portion is much elongated and contractile; salt water, attached or parasitic.

P. clymenellae (Shumway) (Fig. 279, h). 100 μ long; in colon of *Clymenella troquata*; Woods Hole.

Genus **Glossatella** Bütschli. With a large adoral membrane; often attached to fish and amphibian larvae.

G. tintinnabulum (Kent) (Fig. 280, a). 30–43 μ long; attached to epidermis and gills of young Triton.

Genus **Ellobiophrya** Chatton et Lwoff. Posterior end drawn out into 2 arm-like processes by means of which the organism

holds fast to gill bars of the mussel, *Donax vittatus*. One species.

E. donacis C. et L. (Fig. 280, *b*). 50μ by 40μ , excluding the processes.

Family 4 **Epistylidae** Kent

Genus **Epistylis** Ehrenberg. Inverted bell-form; usually individuals on dichotomous non-contractile stalk, forming large colonies; attached to fresh or salt water animals. Numerous species.

E. plicatilis E. (Fig. 280, *c*). $90\text{--}100\mu$ long; colony often up to 3 mm. in height; fresh water.

E. fugitans Kellicott (Fig. 280, *d*). $50\text{--}60\mu$ long; attached to *Sida* in early spring; Niagara river, N. Y.

E. cambari K. (Fig. 280, *e, f*). About 50μ long; attached to gills of *Cambarus*; Niagara river, N. Y.

Genus **Rhabdostyla** Kent. Similar to *Epistylis*; but solitary with a non-contractile stalk; attached to aquatic animals in fresh or salt water. Numerous species.

R. vernalis Stokes (Fig. 280, *g*). About 50μ long; attached to *Cyclops* and *Cypris* in pools in early spring.

Genus **Opisthostyla** Stokes. Similar to *Rhabdostyla*; but stalk long and bent at its point of attachment to submerged object, and acts like a spring; fresh or salt water.

O. annulata S. (Fig. 280, *h*). Body about 23μ long; fresh water.

Genus **Campanella** Goldfuss. Similar to *Epistylis*; but adoral double zone turns 4–6 times; fresh water.

C. umbellaria (Linnaeus) (Fig. 280, *i*). Colony may reach several millimeters in height; individuals $130\text{--}350\mu$ long (Kent).

Genus **Pyxidium** Kent. Stalk simple, not branching; peristome even when fully opened, not constricted from the body proper; frontal disk small, oblique, supported by style-like slender process arising from peristome; attached to freshwater animals and in vegetation.

P. vernale Stokes (Fig. 280, *j*). Solitary or few together; $70\text{--}85\mu$ long; fresh water among algae.

P. urceolatum S. (Fig. 280, *k*). About 90μ long; fresh water on plants.

Genus **Opercularia** Stein. Individuals similar to *Pyxidium*; but short stalk dichotomous; peristome border like a band.

O. stenostoma S. (Fig. 280, l). When extended up to 125μ long; attached to *Asellus aquaticus* and others.

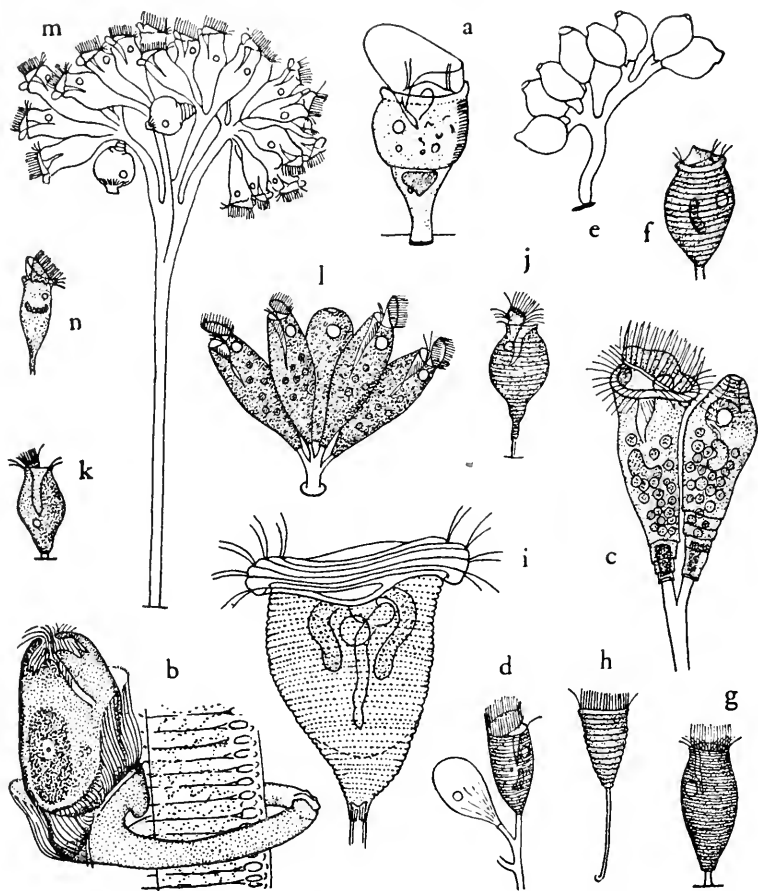


FIG. 280. a, *Glossatella tintinnabulum*, $\times 610$ (Penard); b, *Ellobiophrya donacis*, $\times 900$ (Chatton and Lwoff); c, *Epistylis plicatilis*, $\times 200$ (Stein); d, *E. fugitans*, $\times 260$ (Kellicott); e, f, *E. cambri* (e, $\times 140$; f, $\times 340$) (Kellicott); g, *Rhabdostyla vernalis*, $\times 320$ (Stokes); h, *Opisthostyla annulata*, $\times 440$ (Stokes); i, *Campanella umbellaria*, $\times 180$ (Schröder); j, *Pyridium vernale*, $\times 240$ (Stokes); k, *P. urceolatum*, $\times 140$ (Stokes); l, *Opercularia stenostoma*, $\times 140$ (D'Udekem); m, n, *O. plicatilis* (m, $\times 40$; n, $\times 60$) (Stokes).

O. plicatilis Stokes (Fig. 280, m, n). About 254μ long; colony 1.25–2.5 mm. high; pond water.

Family 5 Vorticellidae Fromental

Genus *Vorticella* Linnaeus. Inverted bell-form; colorless, yellowish, or greenish; peristome more or less outwardly extended; pellicle sometimes annulated; with a contractile stalk, macro-

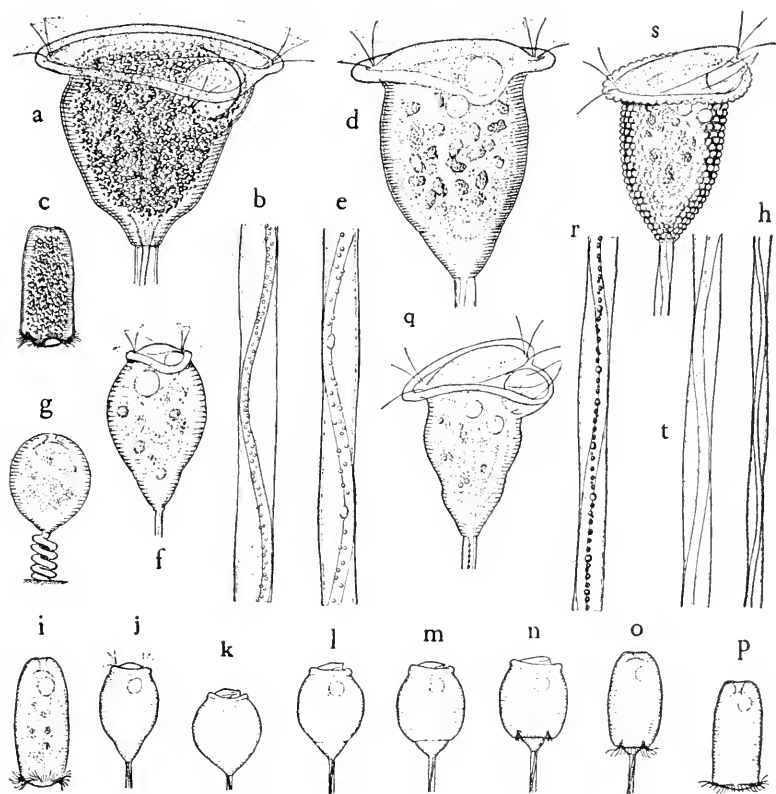


FIG. 281. a-c, *Vorticella campanula* (a, $\times 400$; b, part of stalk, $\times 800$; c, telotroch, $\times 200$); d, e, *V. convallaria* (d, $\times 400$; e, $\times 800$); f-p, *V. microstoma* (f, g, $\times 400$; h, $\times 840$; i, telotroch, $\times 400$; j-p, telotroch-formation *in vitro*, $\times 270$); q, r, *V. picta* (q, $\times 400$; r, $\times 800$); s, t, *V. monilata* (s, $\times 400$; t, $\times 800$) (All, Noland and Finley).

nucleus band-form; micronucleus; 1-2 contractile vacuoles; solitary; in fresh or salt water, attached to submerged objects. Noland and Finley (1931) gave an excellent taxonomic consideration of the genus. Numerous species.

V. campanula Ehrenberg (Fig. 281, *a-c*). Usually in groups; endoplasm filled with refractile reserve granules; vestibule very large with an outer pharyngeal membrane; $50-157\mu$ by $35-99\mu$; peristome $60-125\mu$ wide; stalk $50-4150\mu$ by $5.6-12\mu$; fresh water.

V. convallaria (L.) (Fig. 281, *d, e*). Resembles the last-named species; but anterior end somewhat narrow; usually without refractile granules in endoplasm; $50-95\mu$ by $35-53\mu$; peristome $55-75\mu$ wide; stalk $25-460\mu$ by $4-6.5\mu$; fresh water.

V. microstoma Ehrenberg (Fig. 281, *f-p*). $35-83\mu$ by $22-50\mu$; peristome $12-25\mu$ wide; stalk $20-385\mu$ by $1.5-4\mu$; common in freshwater infusion.

V. picta (E.) (Fig. 281, *q, r*). $41-63\mu$ by $20-37\mu$; peristome $35-50\mu$; stalk $205-550\mu$ by $4-7\mu$; 2 contractile vacuoles; with refractile granules in stalk; fresh water.

V. monilata (Tatem) (Fig. 281, *s, t*). Body with pellicular tubercles; 2 contractile vacuoles; $50-78\mu$ by $35-57\mu$; peristome $35-63\mu$ wide; stalk $50-200\mu$ by $5-6.5\mu$; fresh water.

Genus **Carchesium** Ehrenberg. Similar to *Vorticella*; but colonial; myonemes in stalk not continuous, and therefore individual stalks contract independently; attached to fresh or salt water animals or plants; occasionally colonies up to 4 mm. high. Several species.

C. polypinum (Linnaeus) (Figs. 34; 282, *a*). $100-125\mu$ long; fresh water.

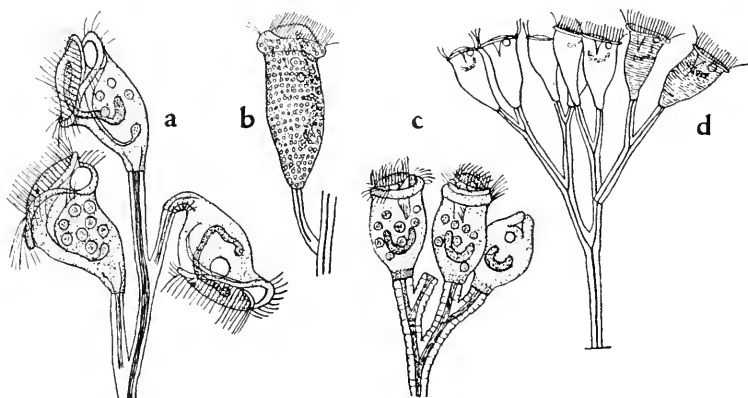


FIG. 282. *a*, *Carchesium polypinum*, $\times 200$ (Stein); *b*, *C. granulatum*, $\times 220$ (Kellicott); *c*, *Zoothamnium arbuscula*, $\times 200$ (Stein); *d*, *Z. adamsi*, $\times 150$ (Stokes).

C. granulatum Kellicott (Fig. 282, *b*). About 100μ long; 2 contractile vacuoles anterior; on *Cambarus* and aquatic plants; Niagara river, N. Y.

Genus **Zoothamnium** Bory. Similar to *Carchesium*; but myonemes (Fig. 15) of all stalks of a colony are continuous with one another, so that the entire colony contracts or expands simultaneously; fresh or salt water; colonies sometimes several millimeters high. Numerous species.

Z. arbuscula Ehrenberg (Fig. 282, *c*). $40\text{--}60\mu$ long; colony up to more than 6 mm. high; fresh water.

Z. adamsi Stokes (Fig. 282, *d*). About 60μ long; colony about 250μ high; attached to *Cladophora*; Niagara river, N. Y.

Tribe 2 **Loricata** Kahl

Peristomal margin not connected with lorica; body attached only at posterior end, and extends out, of lorica.....

..... Family 1 Vaginicolidae

Peristomal margin connected with inner margin of aperture of lorica; stalked disk extends out of lorica only.....

..... Family 2 Lagenophryidae (p. 625)

Family 1 **Vaginicolidae** Kent

Genus **Vaginicola** Lamarek. Lorica without stalk, attached to substratum directly with its posterior end; body elongate and cylindrical; fresh or salt water. Numerous species.

V. leptostoma Stokes (Fig. 283, *a*). Lorica about 160μ high; when extended, about $1/3$ of body protruding; on algae in pond water.

V. annulata S. (Fig. 283, *b*). Lorica about 120μ high; below middle, a ring-like elevation; anterior $1/3$ of body protruding, when extended; pond water.

Genus **Cothurnia** Ehrenberg. Similar to *Vaginicola*; but lorica stands on a short stalk; fresh or salt water. Numerous species.

C. canthocampti Stokes (Fig. 283, *c*). Lorica about 80μ high; on *Canthocamptus minutus*.

C. annulata S. (Fig. 283, *d*). Lorica about 55μ high; fresh water.

Genus **Thuricola** Kent. Body and lorica as in *Vaginicola*; but lorica with a simple or complex valve-like apparatus which closes obliquely after the manner of a door when protoplasmic body contracts; salt or fresh water.

T. folliculata (Müller) (Fig. 283, e). Lorica 127–170 μ high (Kent); 160–200 μ high (Kahl); salt and fresh water.

Genus **Thuricolopsis** Stokes. Lorica with an internal, narrow, flexible valve-rest, adherent to lorica wall and projecting across cavity to receive and support the descended valve; protoplasmic body attached to lorica by a pedicle; on freshwater plants.

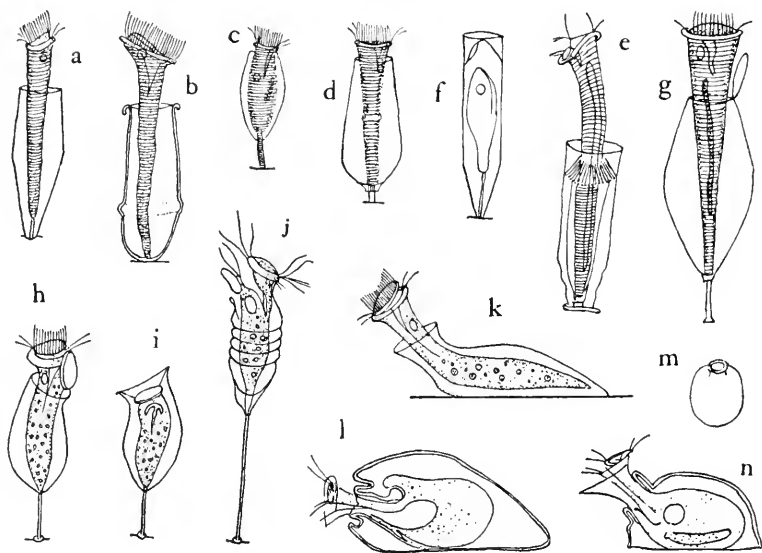


FIG. 283. a, *Vaginicola leptostoma*, $\times 130$ (Stokes); b, *V. annulata*, $\times 170$ (Stokes); c, *Cothurnia canthocampti*, $\times 150$ (Stokes); d, *C. annulata*, $\times 340$ (Stokes); e, *Thuricola folliculata*, $\times 110$ (Kahl); f, *Thuricolopsis kellicottiana*, $\times 110$ (Stokes); g, *Caulicola valvata*, $\times 760$ (Stokes); h, i, *Pyxicola affinis*, $\times 170$ (Kent); j, *P. socialis*, $\times 170$ (Kent); k, *Platycola longicollis*, $\times 200$ (De Fromental); l, *Lagenophrys vaginicola*, $\times 380$ (Penard); m, *L. patina*, $\times 150$ (Stokes); n, *L. labiata*, $\times 340$ (Penard).

T. kellicottiana S. (Fig. 283, f). Lorica about 220 μ long.

Genus **Caulicola** Stokes. Similar to *Thuricola*; but lorica-lid attached to aperture; fresh or brackish water. 2 species.

C. valvata S. (Fig. 283, g). Lorica about 50 μ high; stalk about 1/2; body protrudes about 1/3 when extended; brackish water.

Genus **Pyxicola** Kent. Body attached posteriorly to a corneous lorica; lorica colorless to brown, erect, on a pedicle; a discoidal corneous operculum developed beneath border of peristome,

which closes lorica when organism contracts; fresh or salt water. Many species.

P. affinis K. (Fig. 283, *h, i*). Lorica about 85μ long; in marsh water.

P. socialis (Gruber) (Fig. 283, *j*). Lorica about 100μ long; often in groups; salt water.

Genus **Platycola** Kent. Body similar to that of *Vaginicola*; but lorica always decumbent and attached throughout entire one side to its fulcrum of support; fresh or salt water. Many species.

P. longicollis K. (Fig. 283, *k*). Lorica yellow to brown when older; about 126μ long; fresh water.

Family 2 **Lagenophryidae** Bütschli

Genus **Lagenophrys** Stein. Lorica with flattened adhering surface, short neck and convex surface; "striped body" connects body with lorica near aperture; attached to fresh or salt water animals. Many species.

L. vaginicola S. (Fig. 283, *l*). Lorica 70μ by 48μ ; attached to caudal bristles and appendages of *Cyclops minutus* and *Canthocamptus* sp.

L. patina Stokes (Fig. 283, *m*). Lorica 55μ by 50μ ; on Gammarus.

L. labiata S. (Fig. 283, *n*). Lorica 60μ by 55μ ; on Gammarus.

Suborder 2 **Mobilia** Kahl

Family **Urceolariidae** Stein

Genus **Urceolaria** Lamarek. Peristome more or less obliquely placed; external ciliary ring difficult to see; horny corona of attaching disk with obliquely arranged simple teeth without radial processes; commensal. A few species.

U. mitra (Siebold) (Fig. 284, *a*). 80 – 140μ long; on planarians.

U. paradoxa (Claparède et Lachmann) (Fig. 284, *b*). 70 – 80μ in diameter; colonial forms; in respiratory cavity of *Cyclostoma elegans*.

Genus **Trichodina** Ehrenberg. Low barrel-shaped; with a row of posterior cilia; horny ring of attaching disk with radially arranged hooked teeth; commensal on, or parasitic in, aquatic animals. Several species.

T. pediculus (Müller) (Fig. 284, *c*). A shallow constriction in middle of body; 50 – 70μ in diameter; on Hydra, amphibian larvae

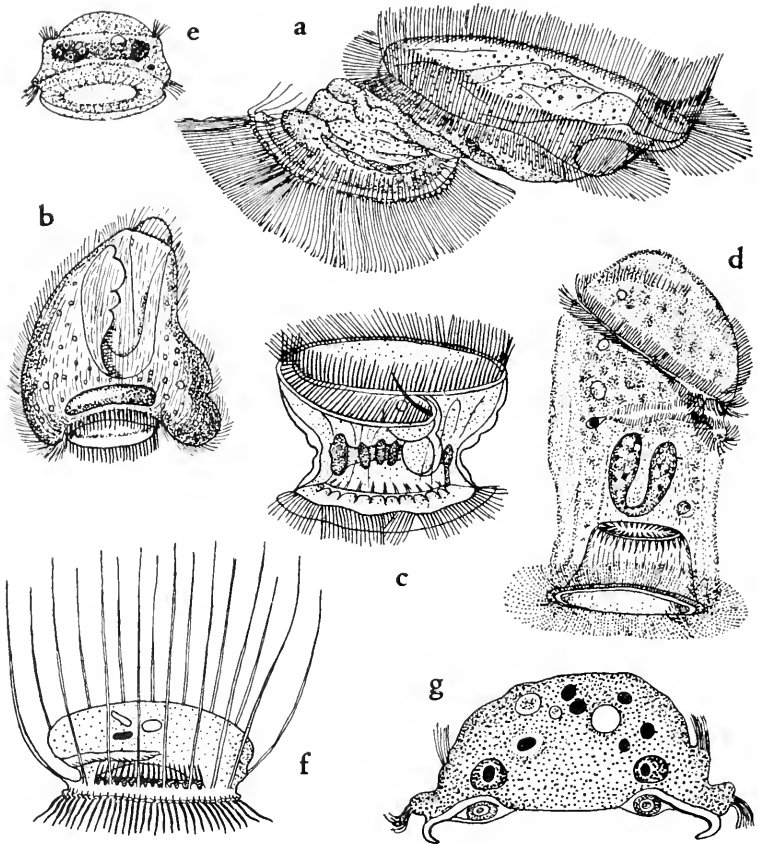


FIG. 284. a, *Urceolaria mitra*, $\times 340$ (Wallengren); b, *U. paradoxa*, $\times 270$ (Claparède and Lachmann); c, *Trichodina pediculus*, $\times 530$ (James-Clark); d, *T. urinicola*, $\times 590$ (Fulton); e, *T. sp.*, $\times 600$ (Diller); f, *Cyclochaeta spongillae*, $\times 600$ (Jackson); g, *C. domerguei*, $\times 800$ (Wallengren).

and probably fish. Those found on *Hydra* and gills of *Necturus* and *Triturus* larvae are probably identical (Fulton, 1923).

T. urinicola Fulton (Fig. 284, d). 50–90 μ long; teeth 28–36; in urinary bladder of a moribund *Bufo* sp. and *Triturus*.

T. sp. Diller (Fig. 284, e). 30–40 μ in diameter; on skin and gills of frog and toad tadpoles.

Genus *Cyclochaeta* Jackson. Similar to *Trichodina*; but bristles or cirri surrounding attaching organella distinctly visible; com-

mensal on, or parasitic in, fresh or salt water animals. Several species.

C. spongillae J. (Fig. 284, *f*). About 60μ in diameter; in interstices of *Spongilla fluviatilis*.

C. domerguei Wallengren (Fig. 284, *g*). About 55μ in diameter; on freshwater fishes.

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CHAPTER 43

Class 2 **Suctoria** Claparède et Lachmann

THE Suctoria which are also known as Acineta, Acinetaria, Tentaculifera, etc., do not possess any cilia or any other cell-organs of locomotion in the mature stage. The cilia are present only on young individuals which are capable of free-swimming, and lost with the development of a stalk or attaching disk, and of tentacles. Therefore, an adult suctorian is incapable of active movement. The body may be spheroidal, elliptical, or dendritic; and is covered with a pellicle and occasionally possesses a lorica. There is no cytostome, and the food-capturing is carried on exclusively by the tentacles. Tentacles are of two kinds: one is suctorial in function and bears a rounded knob on the extremity and the other is for piercing through the body of a prey and more or less sharply pointed. The tentacles may be confined to limited areas or may be distributed over the entire body surface. The food organisms are usually small ciliates and nutrition thus is holozoic.

Asexual reproduction is by binary fission or by budding. The buds which are formed by either exogenous or endogenous gemmation are ciliated, and swim around actively after leaving the parent individual. Finally becoming attached to a suitable object, the buds metamorphose into adult forms. Sexual reproduction is through fusion.

The Suctoria live attached to animals, plants or non-living matter submerged in fresh or salt water, although a few are parasitic.

With only suctorial tentacles

Body irregular or branching

Without proboscis or special arms; often with stolen; without stalk..... Family 1 Dendrosomidae (p. 629)

With proboscis or special arms

With retractile processes bearing tentacles..... Family 2 Ophryodendridae (p. 632)

With branched arms..... Family 3 Dendrocometidae (p. 632)

Body more or less bilaterally symmetrical

Exogenous budding and division..... Family 4 Podophryidae (p. 632)

Endogenous budding

Pellicle thin; with or without lorica; with or without stalk...
 Family 5 Acinetidae (p. 634)

Pellicle thick; without lorica; tentacles a few, variable in form;
 stalk short, stout..... Family 6 Discophryidae (p. 638)

With suctorial and prehensile tentacles; with or without lorica; exogenous budding; commensal on marine hydroids.....
 Family 7 Ephelotidae (p. 641)

Family 1 **Dendrosomidae** Bütschli

Genus **Dendrosoma** Ehrenberg. Dendritic; often large; nucleus band-form, branched; numerous contractile vacuoles; fresh water.

D. radians E. (Fig. 285, *a*). Brownish; 1.2–2.5 mm. high; on vegetation.

Genus **Trichophrya** Claparède et Lachmann. Body small; rounded or elongate, but variable; without stalk; tentacles in fascicles, not branching; endogenous multiple budding; fresh or salt water.

T. epistylidis C. et L. (*T. sinuosa* Stokes) (Fig. 285, *b*). Form irregular; with many bundles of tentacles; nucleus band-form, curved; numerous vacuoles; up to 240 μ long; on *Epistylis*, etc., in fresh water.

T. salparum Entz (Fig. 285, *c*). On various tunicates such as *Molgula manhattensis*; 40–60 μ long; tentacles in 2 groups; salt water; Woods Hole (Calkins).

T. columbiae Wailes (Fig. 285, *d*). 60–75 μ by 40–48 μ in diameter; cylindrical; tentacles at ends; nucleus spherical; in marine plankton; Vancouver (Wailes).

Genus **Astrophrya** Awerinzew. Stellate; central portion drawn out into 8 elongate processes, each with a fascicle of tentacles; body covered by sand grains and other objects. One species.

A. arenaria A. (Fig. 285, *e*). 145–188 μ in diameter; processes 80–190 μ long; in Volga river plankton.

Genus **Lernaeophrya** Pérez. Body large; with numerous short prolongations, bearing very long multifasciculate tentacles; nucleus branched; brackish water. One species.

L. capitata P. (Fig. 285, *f*). Attached to hydrozoan, *Cordylophora lacustris* in brackish water; 400–500 μ long; tentacles 400 μ long.

Genus **Dendrosomides** Collin. Branched body similar to *Dendrosoma*, but with a peduncle; reproduction by budding of vermicular form; salt water. One species.

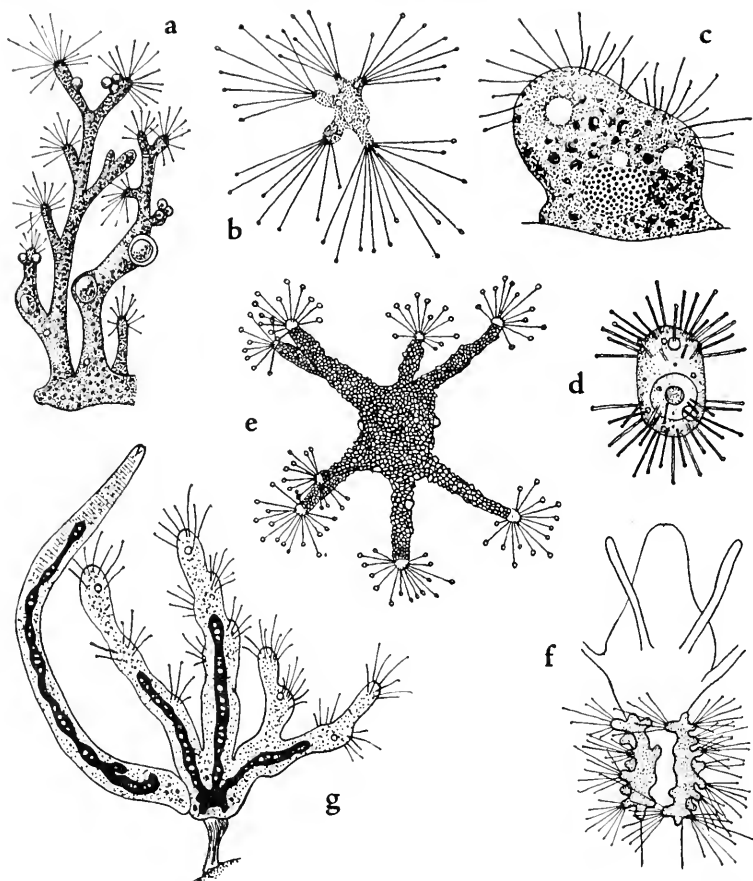


FIG. 285. a, *Dendrosoma radians*, $\times 35$ (Kent); b, *Trichophrya epistylidis*, $\times 250$ (Stokes); c, *T. salparum*, $\times 170$ (Collin); d, *T. columbiae*, $\times 200$ (Wailes); e, *Astrophrya arenaria*, $\times 65$ (Awerinzew); f, *Lernaeophrya capitata*, $\times 35$ (Pérez); g, *Dendrosomides paguri*, $\times 200$ (Collin).

D. paguri C. (Fig. 285, g). 200–300 μ long; vermicular forms 350 μ long; on the crabs, *Eupagurus excavatus* and *E. cuanensis*.

Genus **Rhabdophrya** Chatton et Collin. Elongate, rod-form; with short peduncle, not branched; tentacles distributed over entire surface; macronucleus ellipsoid; micronucleus small; 2–3 contractile vacuoles; salt or brackish water. Several species.

R. trimorpha C. et C. (Fig. 286, a). Up to 150 μ long; on the copepod, *Cletodes longicaudatus*.

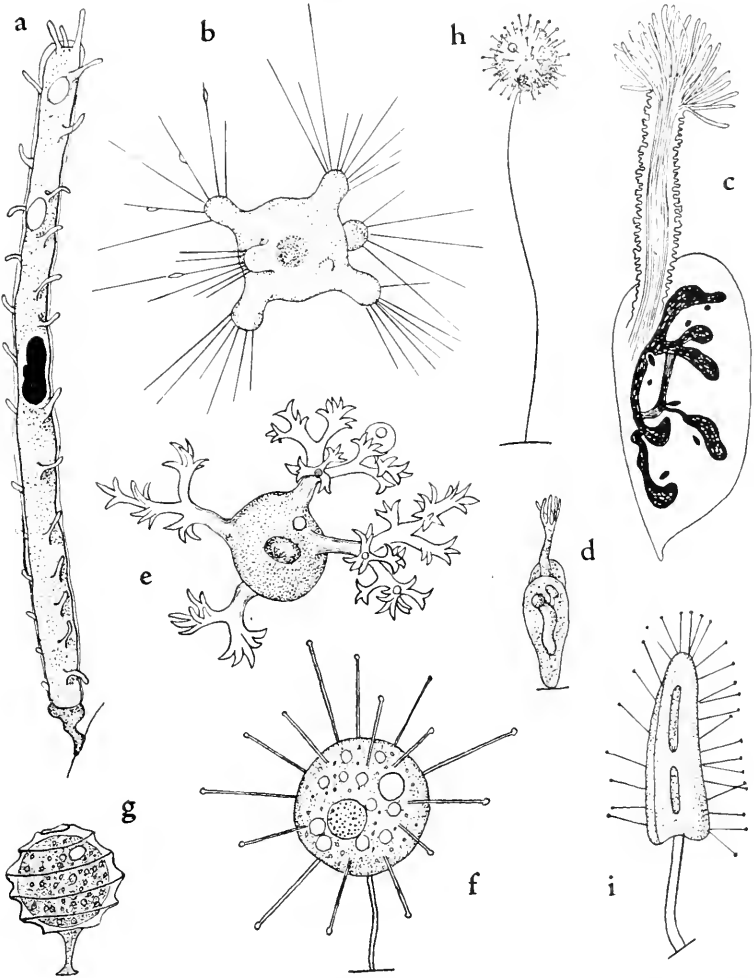


FIG. 286. a, *Rhabdophrya trimorpha*, $\times 650$ (Collin); b, *Staurophrya elegans*, $\times 300$ (Zacharias); c, *Ophryodendron porcellanum*, $\times 330$ (Collin); d, *O. belgicum*, $\times 270$ (Fraipont); e, *Dendrocometes paradoxus*, $\times 270$ (Wrzesnowski); f, g, *Podophrya fixa* (f, $\times 600$ (Wailes); g, $\times 330$ (Collin)); h, *P. gracilis*, $\times 1000$ (Collin); i, *P. elongata*, $\times 240$ (Wailes).

Genus **Staurophrya** Zacharias. Rounded body drawn out into 6 processes.

S. elegans Z. (Fig. 286, b). Tentacles not capitate; macronucleus round; 1-2 contractile vacuoles; about 50μ in diameter; in fresh water.

Family 2 **Ophryodendridae** Stein

Genus **Ophryodendron** Claparède et Lachmann. With one long or 3–6 shorter retractile processes, bearing suckorial tentacles; on Crustacea, Annelida, etc.; salt water. Several species.

O. porcellanum Kent (Fig. 286, c). 60–100 μ long; on *Porcellana platycheles*, etc.

O. belgicum Fraipont (Fig. 286, d). 38–114 μ long; vermicular form 100 μ ; on Bryozoa and hydrozoans; Vancouver (Wailes).

Family 3 **Dendrocometidae** Stein

Genus **Dendrocometes** Stein. Body rounded; with variable number of branched arms; fresh water.

D. paradoxus S. (Fig. 286, e). Up to 100 μ long; on gills of *Gammarus pulex*, *G. puteanus*, etc.

Genus **Stylocometes** Stein. Arms not branched; tentacles finger-like; fresh water.

S. digitatus (Claparède et Lachmann). Up to 110 μ long; on gills of *Asellus aquaticus* and on *Aphrydium versatile*.

Family 4 **Podophryidae** Bütschli

Genus **Podophrya** Ehrenberg. Subspherical; normally with a rigid stalk; suckorial tentacles in fascicles or distributed on entire body surface; encystment common; fresh or salt water. Many species.

P. fixa Müller (Fig. 286, f, g). Spherical; tentacles of various lengths; stalked; nucleus spheroid; one contractile vacuole; 10–28 μ long; fresh water.

P. collini Root. Ovoid; stalked; 30–60 capitate tentacles, distributed; nucleus spherical; one contractile vacuole; 40–50 μ in diameter; in swamp.

P. gracilis Calkins (Fig. 286, h). Small; spherical; long filiform stalk; 1–2 contractile vacuoles; nucleus near attachment of stalk; 8 μ in diameter; stalk 40 μ long; salt water; Woods Hole.

P. elongata Wailes (Fig. 286, i). Elongate; flattened; with a pedicel; tentacles distributed; nucleus cylindrical; 95–105 μ long; stalk 65–85 μ by 7–9 μ ; on the marine copepod, *Euchaeta japonica*; Vancouver.

Genus **Parapodophrya** Kahl. Spherical; tentacles radiating, a few long, more or less conical at proximal portion; stalk thin; salt water.

P. typha K. (Fig. 287, *a*). 50–60 μ in diameter; salt water.

Genus **Sphaerophrya** Claparède et Lachmann. Spherical, without stalk; with or without distributed tentacles; multiplication by binary fission or exogenous budding; fresh water, free-living or parasitic.

S. soliformis Lauterborn (Fig. 287, *b*). Spherical; numerous tentacles about 1/4–1/3 the body diameter; a contractile vacuole; nucleus oval; diameter about 100 μ ; sapropelic.

S. magna Maupas. Spherical; about 50 μ in diameter; numerous tentacles of different length; nucleus spheroid; standing fresh water with decaying vegetation.

S. stentoris M. Parasitic in Stentor; swarmers ciliated on posterior end; the other end with capitate tentacles; nucleus spheroid; 2 contractile vacuoles; about 50 μ long.

Genus **Paracineta** Collin. Spherical to ellipsoidal; tentacles distributed; mostly in salt water, a few in fresh water.

P. limbata (Maupas) (Fig. 287, *c, d*). With or without gelatinous envelope; 20–50 μ in diameter; swarmer with many ciliated bands, contractile; on plants and animals in salt water.

Genus **Metacineta** Bütschli. Lorica funnel-shaped, lower end drawn out for attachment; tentacles grouped at anterior end; nucleus spherical; one contractile vacuole. One species.

M. mystacina (Ehrenberg) (Fig. 287, *e*). Lorica up to 700 μ long; in fresh and salt water.

Genus **Urmula** Claparède et Lachmann. Lorica colorless; lower end pointed, attached; aperture narrowed, round or triangular; body more or less filling lorica; 1–2 (up to 5) long active tentacles; nucleus central, oval; one or more contractile vacuoles; fresh water.

U. epistylidis C. et L. (Fig. 287, *f*). Up to 80 μ long; on Epistylis, Dendrosoma, etc.

Genus **Lecanophrya** Kahl. Body rounded rectangular in cross-section; anterior region bowl-shaped; somewhat rigid tentacles located on inner surface of bowl; salt water.

L. drosera K. (Fig. 287, *g*). 40–70 μ high; hollow stalk; tentacles in 3–5 indistinct rows; attached to antennae of the copepod, *Nitocra typica*.

Genus **Ophryocephalus** Wailes. Spheroidal, stalked; a single long mobile, capitate tentacle; multiplication by multiple exogenous budding from apical region; on *Ephelota gemmipara* and *E. coronata* (p. 641); salt water. One species.

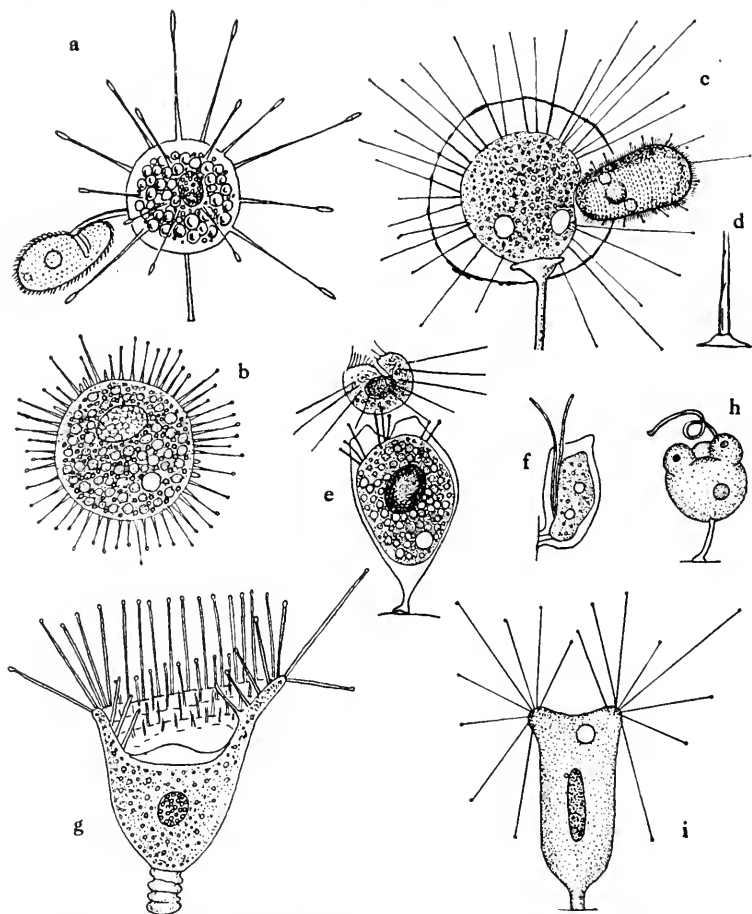


FIG. 287. a, *Parapodophrya typha*, $\times 270$ (Kahl); b, *Sphaerophrya soliformis*, $\times 200$ (Lauterborn); c, d, *Paracineteta limbata* (c, a bud is ready to leave; d, basal part of stalk), $\times 460$ (Collin); e, *Metacineteta mystacina*, capturing *Halteria*, $\times 400$ (Collin); f, *Urmula epistylidis*, $\times 140$ (Claparède and Lachmann); g, *Lecanophrya drosera*, $\times 390$ (Kahl); h, *Ophryocyphalus capitatum*, $\times 200$ (Wailles); i, *Acineteta lacustris*, $\times 200$ (Stokes).

O. capitatum W. (Fig. 287, h). About 55μ long; tentacle up to 100μ by $1.5-5\mu$; Vancouver.

Family 5 Acinetidae Bütschli

Genus *Acineteta* Ehrenberg. Lorica more or less flattened; usually with stalk; tentacles in 2 (1 or 3) bundles; body completely

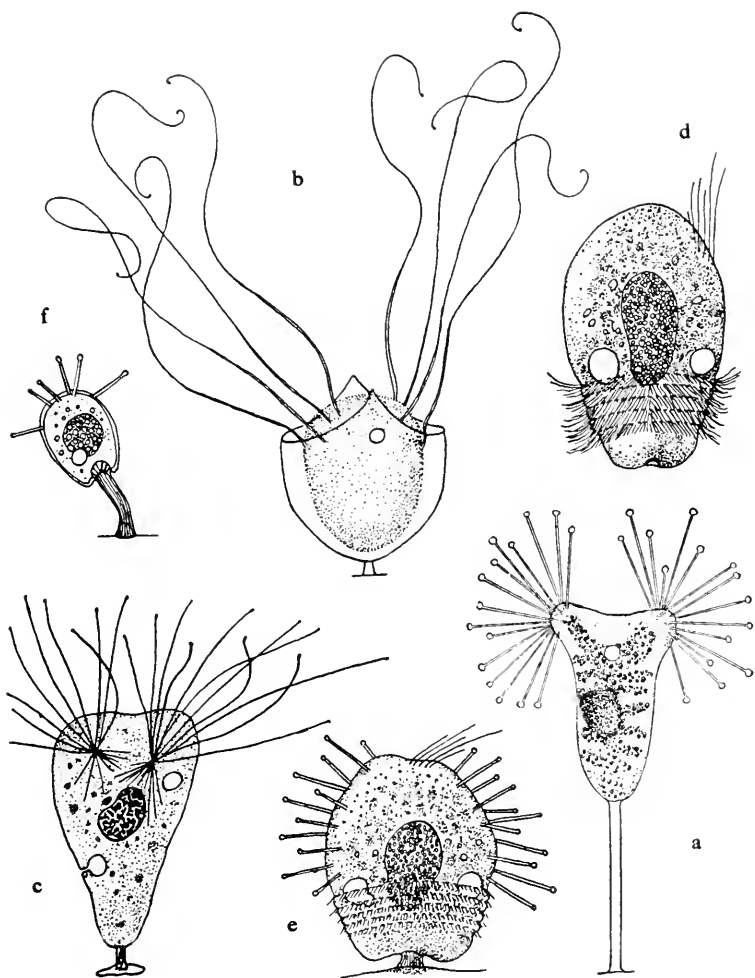


FIG. 288. a, *Acineta tuberosa*, $\times 670$ (Calkins); b, *A. cuspidata*, $\times 670$ (Stokes); c-e, *Tokophrya infusionum* (c, $\times 400$; d, a free-swimming bud; e, a young attached form, $\times 800$) (Collin); f, *T. cyclosum*, a young individual, $\times 500$ (Collin).

or partly filling lorica; swarmer with ciliated band or completely ciliated; fresh or salt water. Numerous species.

A. tuberosa E. (Fig. 288, a). Lorica 50–100 μ high; with stalk; salt and brackish water.

A. cuspidata Stokes (Fig. 288, b). Lorica cup-shaped; front

end with 2 opposing sharp points; lorica 32–42 μ high; on *Oedogonium* in fresh water.

A. lacustris S. (Fig. 287, *i*). Lorica elongate ovoid; flattened; 75–185 μ high; on *Anacharis* in pond.

Genus **Tokophrya** Büttsehli. Pyriform or pyramidal; without lorica; tentacles in 1–4 bundles on anterior surface; stalk soft; swimmers oval, with several ciliary bands and long cilia; fresh water. Several species.

T. infusionum (Stein) (Fig. 288, *c–e*). Inverted pyramid; stalk with or without attaching disk; macronucleus oval; 2 contractile vacuoles; about 60 μ long.

T. cyclopum (Claparède et Lachmann) (Fig. 288, *f*). Oval or spherical; stalk short; tentacles in 2–5 bundles; macronucleus spherical; 1–2 contractile vacuoles; about 50 μ long; on *Cyclops*, etc.

Genus **Thecacineta** Collin. Lorica with free margin; body usually attached to bottom of lorica, more or less long; tentacles from anterior end; salt water. Several species.

T. cothurnioides C. (Fig. 289, *a*). Lorica about 50 μ high; stalk knobbed; on *Cletodes longicaudatus*.

T. gracilis (Wailes) (Fig. 289, *b*). Lorica 110 μ by 35 μ ; stalk 200 μ by 4 μ ; on hydroids.

Genus **Periacineta** Collin. Elongate lorica; attached with its drawn-out posterior end; tentacles from the opposite surface in bundles; fresh water.

P. buckei (Kent) (Fig. 289, *c*). Attached end of lorica with basal plate; 3 contractile vacuoles; up to 125 μ long; on *Lymnaea stagnalis* and *Ranatra linearis*.

Genus **Hallezia** Sand. Without lorica; with or without a short stalk; tentacles in bundles; fresh water.

H. brachypoda (Stokes) (Fig. 289, *d*). 34–42 μ in diameter; in standing water among leaves.

Genus **Solenophrya** Claparède et Lachmann. Lorica attached directly with its under side; body usually not filling lorica; tentacles in bundles; fresh water.

S. inclusa Stokes (Fig. 289, *e*). Lorica subspherical; about 44 μ in diameter; standing fresh water.

S. pera S. (Fig. 289, *f*). Lorica satchel-form; about 40–45 μ high; body about 35 μ long; standing fresh water.

Genus **Acinetopsis** Robin. Lorica in close contact with body

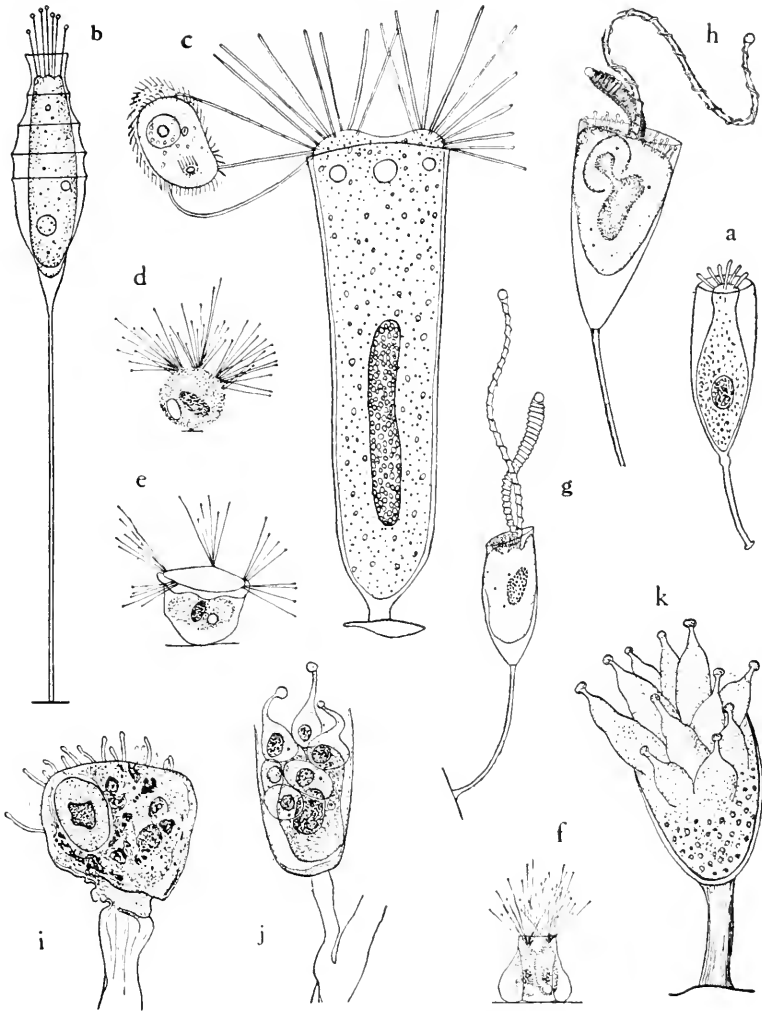


FIG. 289. a, *Thecacincta cothurnioides*, $\times 400$ (Collin); b, *T. gracilis*, $\times 270$ (Wailes); c, *Periacincta buckei*, feeding on *Chilodonella*, $\times 530$ (Collin); d, *Hallezia brachypoda*, $\times 200$ (Stokes); e, *Solenophrya inclusa*, $\times 230$ (Stokes); f, *S. pera*, $\times 230$ (Stokes); g, h, *Acinctopsis tentaculata* (g, $\times 130$; h, $\times 230$) (Root); i, j, *Tachyblaston ephelotensis* (i, a young individual in *Ephelota*, $\times 260$; j, mature form, $\times 500$) (Martin); k, *Dactylophrya roscovita*, $\times 830$ (Collin).

on sides; stalked; 1-6 large retractile tentacles and numerous small tentacles from apical end; mainly salt water.

A. tentaculata Root (Fig. 289, *g, h*). Lorica 187μ high; stalk 287μ long; large tentacles up to 500μ long; body about 138μ by 100μ ; on *Obelia commissuralis* and *O. geniculata*; Woods Hole.

Genus **Tachyblaston** Martin. Lorica with short stalk; tentacles distributed on anterior surface; nucleus oval; salt water. One species.

T. ephelotensis M. (Fig. 289, *i, j*). Lorica $30\text{--}93\mu$ high; stalk $20\text{--}30\mu$ long; attached to *Ephelota gemmipara*.

Genus **Dactylophrya** Collin. Cup-like lorica, filled with the protoplasmic body; with a short stalk; $12\text{--}15$ arm-like tentacles from anterior surface; salt water. One species.

D. roscovita C. (Fig. 289, *k*). About 40μ long excluding stalk; on the hydrozoan, *Diphasia attenuata*.

Genus **Pseudogemma** Collin. Attached with a short stalk to larger suctorians; without tentacles; endogenous budding; swarmer with 4 ciliary bands; salt water.

P. pachystyla C. (Fig. 290, *a*). About 30μ long; stalk $3\text{--}4\mu$ wide; swarmer 15μ by 9μ ; on *Acineta tuberosa*.

Genus **Endosphaera** Engelmann. Spherical; without lorica; without tentacles; budding endogenous; swarmer with 3 equatorial ciliary bands; parasitic in Peritricha; fresh and salt water.

E. engelmanni Entz (Fig. 290, *b*). $15\text{--}41\mu$ in diameter; imbedded in the host's cytoplasm; swarmer $13\text{--}19\mu$ in diameter; in *Opisthonecta henneguyi* (p. 618), and other peritrichs.

Genus **Allantosoma** Gassovsky. With neither lorica nor stalk; elongate; one or more tentacles at ends; macronucleus oval or spherical; compact micronucleus; a single contractile vacuole; cytoplasm often filled with small spheroidal bodies; development unknown; in mammalian intestine.

A. intestinalis G. (Fig. 290, *c*). $33\text{--}60\mu$ by $18\text{--}37\mu$; attached to various ciliates occurring in caecum and colon of horse.

A. dicorniger Hsiung (Fig. 290, *d*). $20\text{--}33\mu$ by $10\text{--}20\mu$; unattached; in colon of horse.

A. brevicorniger H. (Fig. 290, *e*). $23\text{--}36\mu$ by $7\text{--}11\mu$; attached to various ciliates of caecum and colon of horse.

Family 6 Discophryidae Collin

Genus **Discophrya** Lachmann. Elongate; a short stout pedicel with a plate; tentacles evenly distributed on anterior surface or

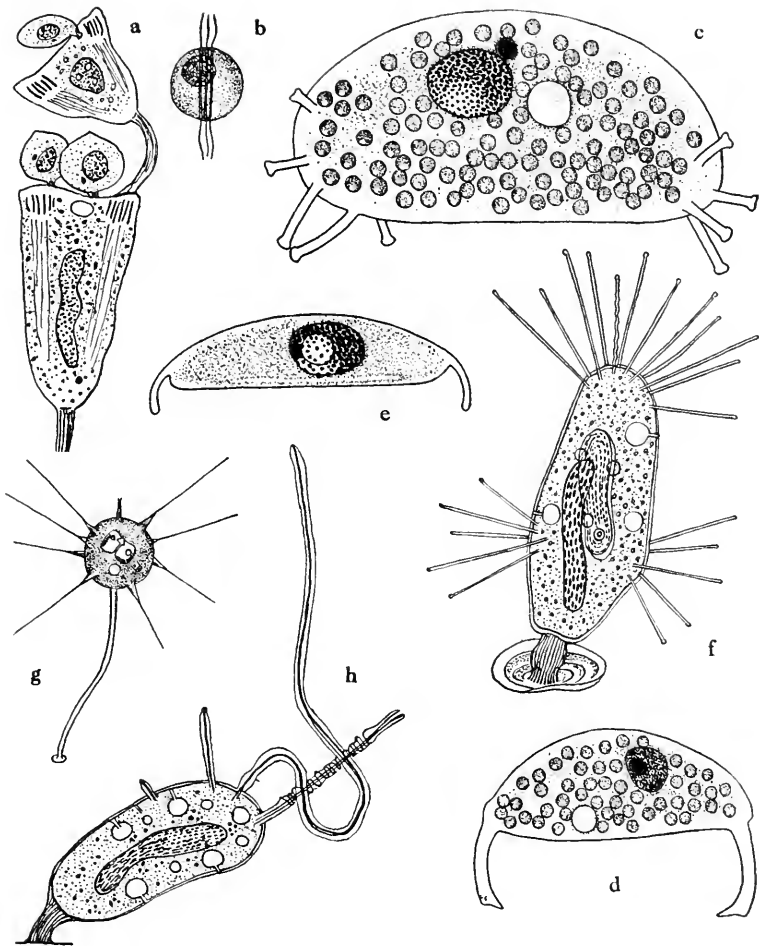


FIG. 290. a, *Pseudogemma pachystyla*, $\times 400$ (Collin); b, *Endosphaera engelmanni*, $\times 500$ (Lynch and Noble); c, *Allantosoma intestinalis*, $\times 1050$ (Hsiung); d, *A. dicorniger*, $\times 1300$ (Hsiung); e, *A. brevicorniger*, $\times 1400$ (Hsiung); f, *Discophrya elongata*, $\times 440$ (Collin); g, *Thaumtophrya troid*, $\times 1150$ (Claparède and Lachmann); h, *Rhynchophrya palpans*, $\times 440$ (Collin).

in bundles; contractile vacuoles, each with canalicule leading to body surface; mainly fresh water. Several species.

D. elongata (Claparède et L.) (Fig. 290, f). Cylindrical; tentacles on anterior end and in 2 posterior bundles; stalk striated; about 80μ long; on shell of *Pauldina vivipara* in fresh water.

Genus **Thaumtophrya** Collin. Spherical; long stalk; tentacles distributed, tapering toward distal end; salt water. One species.

T. troid (Claparède et Lachmann) (Fig. 290, g). About 75μ in diameter.

Genus **Rhynchophrya** Collin. Oblong; bilaterally symmetrical; a short striated stalk; 1 main long and a few shorter tentacles; 6–10 contractile vacuoles, each with a canalicule leading to outside; fresh water. One species.

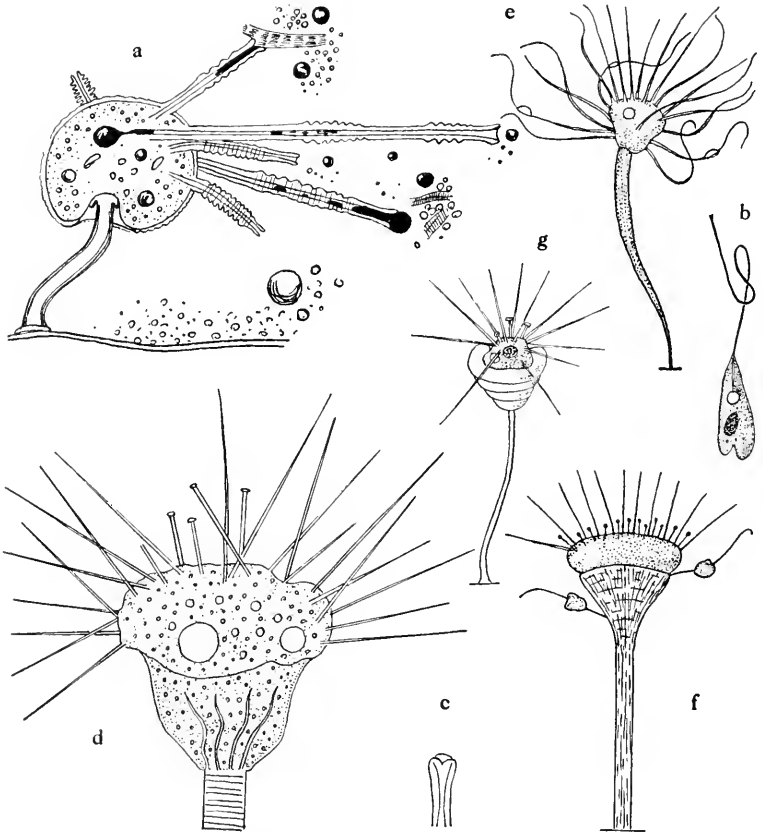


FIG. 291. a, *Choanophrya infundibulifera*, feeding on disintegrating part of a *Cyclops*, $\times 400$ (Collin); b, c, *Rhyncheta cyclopum* (b, $\times 100$; c, end of tentacle, $\times 400$) (Zenker); d, *Ephelota gemmipara*, $\times 200$ (Hertwig); e, *E. coronata*, $\times 140$ (Kent); f, *E. plana*, front view, with two attached *Ophryocephalus*, $\times 35$ (Wailes); g, *Podocyathus diadema*, $\times 200$ (Kent).

R. palpans C. (Fig. 290, *h*). 85μ by 50μ ; tentacles retractile, 10–200 μ long; stalk 20μ by 10μ ; on *Hydrophilus piceus*.

Genus **Choanophrya** Hartog. Spheroidal to oval; stalked; 10–12 tentacles, tubular, expansible at distal end to engulf voluminous food particles; macronucleus oval to spherical; a micronucleus; fresh water. One species.

C. infundibulifera H. (Fig. 291, *a*). 65μ by 60μ ; fully extended tentacles 200 μ long; on *Cyclops ornatus*.

Genus **Rhyncheta** Zenker. Protoplasmic body attached directly to an aquatic animal; with a long mobile tentacle bearing a sucker at its end.

R. cyclopus Z. (Fig. 291, *b, c*). About 170 μ long; on *Cyclops*.

Family 7 Ephelotidae Sand

Genus **Ephelota** Wright. Without lorica; stalk stout, often striated; suctorial and prehensile tentacles distributed; macronucleus usually elongate, curved; on hydroids, bryozoans, algae, etc.; salt water. Numerous species.

E. gemmipara Hertwig (Fig. 291, *d*). About 250 μ by 220 μ ; stalk up to 1.5 mm. long; on hydroids, bryozoans, etc.

E. coronata Kent (Fig. 291, *e*). Flattened; 90–200 μ long; stalk longitudinally striated (Kent); on hydroids, bryozoans, algae, etc.

E. plana Wailes (Fig. 291, *f*). 150–320 μ by 100–150 μ ; stalk 100 μ –1 mm. long; on bryozoans; Vancouver.

Genus **Podocyathus** Kent. Differ from *Ephelota* in having conspicuous lorica; salt water. One species.

P. diadema K. (Fig. 291, *g*). Lorica about 42 μ long; on bryozoans, hydrozoans, etc.

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Author and Subject Index

Numbers in bold-face type indicate pages on which are given the definitions, explanations, and discussions of technical terms; the characterizations or differentiations of taxonomic subdivisions; or the descriptions of genera and species.

Numbers in *italics* indicate pages on which appear those illustrations that could not be placed on the same pages as the related text matter.

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